Universidad de Concepción

Facultad de Ciencias Ambientales
Programa de Doctorado en Ciencias Ambientales con mención en Sistemas Acuáticos Continentales

EFECTOS DE LAS ALTERACIONES DEL RÉGIMEN DE CAUDAL EN LA ESTRUCTURA DE ENSAMBLES DE MACROINVERTEBRADOS Y PECES: UN ENFOQUE TAXONÓMICO Y FUNCIONAL

Tesis para optar al grado de

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ANAYSA VICTORIA ELGUETA HERRERA

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2 INTRODUCCIÓN

2.1 Régimen de caudal natural y alterado y su importancia en sistemas fluviales.

Los asentamientos humanos se han desarrollado históricamente en torno a ríos, en base a la presencia de cuencas hidrográficas, como resultado de los múltiples beneficios o servicios ecosistémicos que éstos aportan a la vida humana (Brauman et al., 2014). El desarrollo de actividades antropogénicas en los sistemas fluviales de todo el mundo no ha estado exento de menoscabo, sino que ha significado un deterioro estructural y cambios en el funcionamiento ecológico de los ríos (Petts & Calow, 1996; Naiman et al., 2008). Un ejemplo de ello es el desarrollo energético en base a la energía potencial del agua de ríos que, a través de su esquema de generación eléctrica, a menudo cambia el régimen de caudal de los ríos, modificando la estructura y funcionamiento de éstos, con consecuencias negativas para los ecosistemas y la biodiversidad (Anderson et al., 2006; Botelho et al., 2017). Numerosos estudios han abordado los efectos de la regulación de caudales sobre los distintos componentes de los sistemas fluviales (Kennedy et al., 2016; Bejarano et al., 2017; Ashraf et al., 2018). Sin embargo, el estudio de los efectos de la sola regulación de caudales no siempre ha permitido entender los cambios que se producen en estos ecosistemas. Más bien ha quedado de manifiesto la complejidad en las respuestas de los ecosistemas fluviales y las comunidades bióticas que habitan en él, poniendo en evidencia la necesidad de estudios desde una perspectiva interdisciplinaria. En este contexto, esta investigación aborda los efectos de la regulación de caudales en una cuenca altamente intervenida por hidroelectricidad desde una perspectiva interdisciplinaria, integrando variables hidrológicas, geomorfológicas y ecológicas. El objetivo es comprender las múltiples interacciones que ocurren en los ríos sometidos a cambios de su régimen de caudal y cómo éstas desencadenan respuestas en las comunidades bióticas. Además, con el fin de obtener un amplio entendimiento de las respuestas bióticas a la regulación de caudales, en esta investigación se analizan comunidades de peces y de macroinvertebrados en distintas zonas dentro de la red hídrica con características de hábitat particulares.

2.2 El régimen de caudal la variable “maestro” de los sistemas fluviales.

El régimen hidrológico se define como la distribución del caudal de un río a lo largo de todo el año y es caracterizado a través de cinco atributos observables, su magnitud, frecuencia, duración, timing y tasa de cambio (Poff et al., 1997). Cada uno de estos atributos son ampliamente utilizados para caracterizar toda la gama de flujos y fenómenos hidrológicos específicos -inundaciones o caudales bajos- que ocurren en los ríos. El régimen de caudal es considerado como el elemento articulador que organiza y define el ecosistema fluvial (Poff et al., 1997). A través de procesos físicos modela la geomorfología fluvial, diseña los cauces, las riberas y en algunos casos la forma del valle. El flujo del agua moviliza los sedimentos disponibles, los restos de madera y otros materiales transportables en el canal y entre el canal y la llanura aluvial. Ello, condiciona a su vez innumerables variables del medio, como la luz, temperatura del agua, la concentración de oxígeno, los nutrientes, la velocidad del agua, el hábitat, la productividad primaria, las cadenas tróficas, la reproducción e interacciones bióticas (Poff et al., 1997). Además, permite el mantenimiento de los patrones naturales de conectividad longitudinal y lateral, esenciales para la viabilidad de las poblaciones de muchas especies ribereñas (Ward et al., 1989; Newbold et al., 1982).

2.3 Alteración de los regímenes de caudal natural y sus efectos en los ecosistemas fluviales.

Hoy en día, diversas actividades antropogénicas alteran el régimen natural del caudal y amenazan la sustentabilidad ecológica de los ríos (Naiman et al., 2008). Entre ellas, destacan actividades tales como la instalación de centrales hidroeléctricas, embalses, extracción de agua, cambios en el uso del suelo, urbanización y canalización de ríos (Naiman et al., 1995; Sparks, 1995; Ward et al., 1999).

Las consecuencias de alterar el régimen de caudal fuera del rango de variación natural se manifiestan a distintos niveles físicos - microhábitat, tramos, cuenca - y ecológicos de organización –comunidades, población, individuos- y se visualizan en diversas y complejas respuestas ecosistémicas. Naiman et al. (2008) exponen que las alteraciones en la magnitud y frecuencia de los caudales provoca cambios en la disponibilidad y complejidad de hábitats, como también pérdida de la conectividad hidrológica, lo que a su vez desencadena sucesivas alteraciones en los patrones de historia de vida de las especies provocando reducciones en la supervivencia de individuos, poblaciones, comunidades y especies de biota acuática. Además, la alteración de la magnitud y frecuencia de las crecidas o sequías tiene como consecuencia el desplazamiento de los organismos de su hábitat natural (deriva) o la pérdida de hábitats en periodos de sequía (Jowett & Richardson, 1989). Se reconoce que la reducción de caudal durante largos periodos de tiempo puede provocar pérdida de la conectividad lateral y longitudinal, contracción del hábitat activo para las especies, disminución de la capacidad de carga del hábitat, aumento en la presión de depredación, cambios sustanciales en la cadena trófica, pérdida de especies reofílicas y sensibles a cambios de temperatura y oxígeno, favorece la dominancia de especies generalistas en el uso de recursos y la generación de nuevos nichos de colonización para especies invasoras, lo cual amenaza a especies nativas sensibles (Poff et al., 1997; Rolls et al., 2012). Por último, la pérdida de los peak estacionales de caudal puede causar interrupción en las señales para el desarrollo de desove, eclosión de los huevos y migraciones de peces, lo que, sumado a la pérdida de acceso a zonas inundadas, modifica la estructura trófica y disminuye el acceso a las áreas de desove y crianza (Poff et al., 1997; Rolls et al., 2012).

Diversos autores han descrito los mecanismos físicos y las respuestas ecológicas que ocurren una vez que los atributos hidrológicos son alterados, tanto para macroinvertebrados como para peces (Cereghino, 1998; Poff, 1997; Rolls et al., 2012; Tabla 2.1.). No obstante, esta evidencia empírica en su mayoría se ha concentrado en escalas espaciales relativamente finas, a escala de tramos, y considerando como medida de análisis la diversidad taxonómica (Bunn &

Arthington, 2002; Poff & Zimmerman, 2010 & Rolls et al., 2018). Mientras que, un limitado número de estudios han abordado las respuestas bióticas a la perturbación de caudal a escalas espaciales superiores y basándose en un análisis enfocado en la diversidad funcional (Tabla 2.1). En este sentido, Rolls et al., 2018, reconoce que la principal brecha de conocimiento en el campo de la eco-hidrología está enfocada principalmente en un análisis simultaneo de la respuesta de la biodiversidad a distintos gradientes hidrológicos y diferentes escalas espaciales.

Tabla 2.1. Respuestas ecológicas a los distintos mecanismos hidrológicos que ocurren en presencia de una alteración de caudal.

Mecanismo hidrológico	**Grupo biótico**	**Métrica evaluada**	**Respuesta ecológica**	**Escala espacial**	**Bibliografía.**
Incremento de la variación caudales	Macroinvertebrados y peces	Taxonómico	Lavado de materia orgánica y biota.	Tramo	Kroger, 1973; Saltveit et al., 2001.
	Peces	Taxonómico	Pérdida de especies sensibles	Cuenca	Gehrke *et al.,* 1995
		Funcional		Tramo	Kingsolving & Bain, 1993; Travnichek et al., 1995
Estabilidad de caudales	Macroinvertebrados y peces	Taxonómico	Invasión especies Amenaza para especies nativas sensibles	Tramo	Nilsson & Bergreen, 2000; Hickerson et al., 2019; Propost et al., 2004.
Pérdida de peaks estacionales	Peces	Funcional	Cambio en la composición funcional a lo largo de gradientes de variabilidad hidrológica, estacionalidad y previsibilidad	Regional	Mims & Olden (2012)
Prolongación de los bajos caudales	Macroinvertebrados	Taxonómico	Reducción de hábitat y concentración de organismos acuáticos Desecación de hábitat	Tramo	Bogan & Lytle (2011) and Fritz & Dodds (2005)

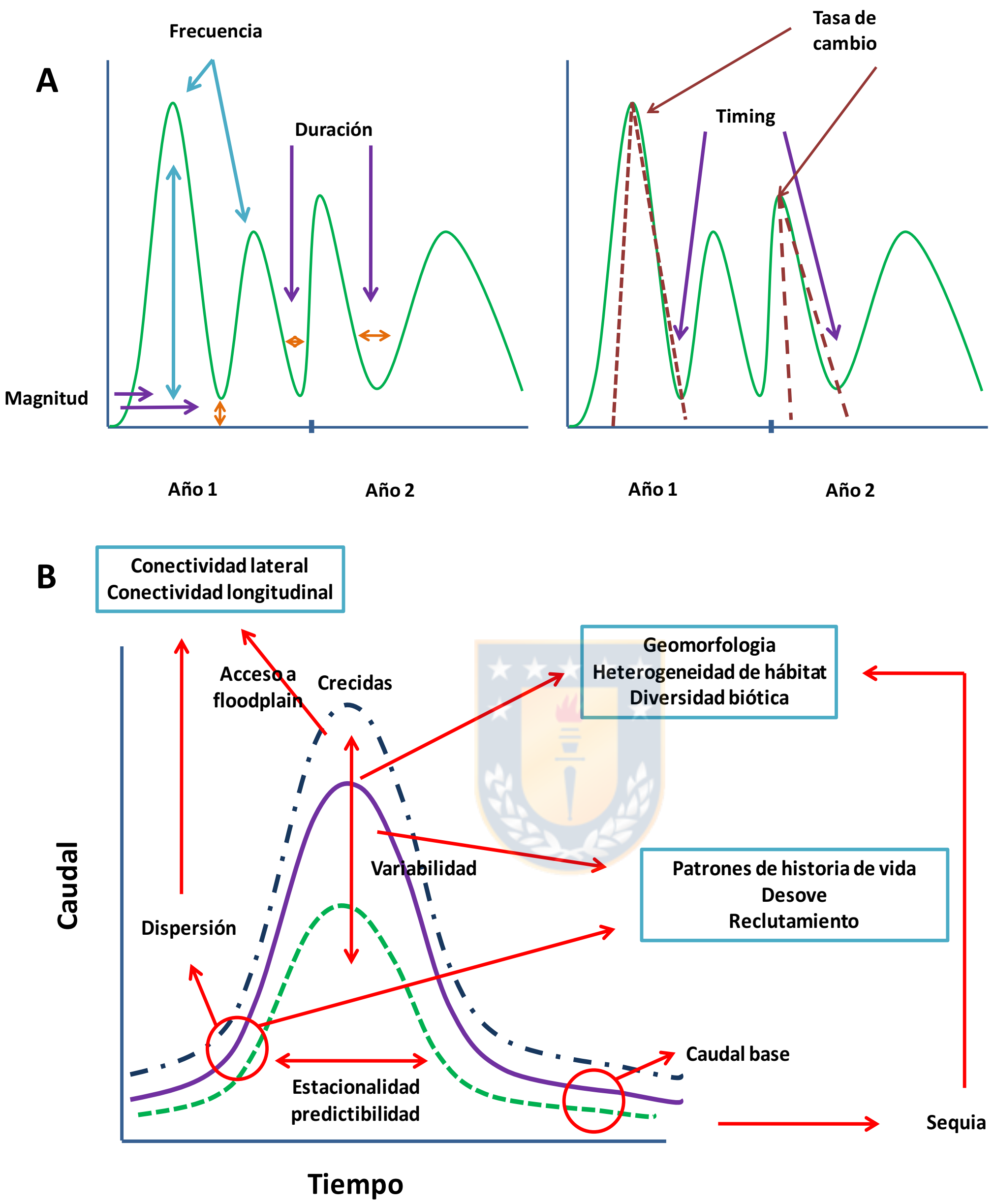

Figura 2.1 A) Representación de los cinco componentes del régimen de caudal. Magnitud: Cantidad de agua de un río. Frecuencia: Ocurrencia de un cierto caudal en un intervalo de tiempo. Duración: Periodo de tiempo en que un cierto caudal ocurre. Timing: Regularidad con que un caudal ocurre. Tasa de cambio: Cuán rápido cambia el caudal de una magnitud a otra. B) Paradigma del régimen natural de caudal (Modificado de Bunn & Arthington, 2002).

2.4 El desarrollo de la hidroelectricidad en Chile.

El desarrollo de la sociedad contemporánea y el futuro del comercio internacional están fuertemente ligados a la disponibilidad de energía. A nivel mundial se prevé que las necesidades de energía aumentarán casi un tercio al año 2035, como respuesta a la mayor demanda de las economías emergentes (Tvaronavieciene et al., 2020). En el caso de Chile, la producción autónoma de energía posee un rol crucial para el crecimiento económico, es así como el país pasó de importar el 60% de la energía al año, a crear en el año 2012 una estrategia de desarrollo energético autónomo, con el objetivo de disminuir la vulnerabilidad del país ante cambios externos en la oferta de energía (cambios en la producción o alzas de precios, Balance Nacional de Energía BNE, 2012). La estrategia de desarrollo energético fomenta el desarrollo autónomo de diversas matrices energéticas de recursos renovables no convencionales, con el fin de aprovechar los recursos naturales en función del mínimo costo alcanzable (Política Energética de Chile, Energía 2050). Bajo esta lógica, el alto potencial hidroeléctrico del país se percibe como una gran oportunidad para la generación de energía, lo que se ha expresado en un explosivo aumento de proyectos de hidroelectricidad presentados y aprobados mediante evaluación ambiental (Habit et al., 2018). En la actualidad el Sistema Eléctrico Nacional en Chile (SEN), abastece más del 90% de la población (desde Arica por el norte hasta Quellón por el sur) con un 30% de energía generada a través de hidroelectricidad (Comisión Nacional de Energía, 2018). Se estima que este porcentaje incrementará a un 51% hacia el año 2030 (Ministerio de Energía, 2016). Los esquemas de operación utilizadas por las centrales hidroeléctricas en Chile se basan en dos tipos: hydropeaking (operación de punta) y run-of-river (operación base). Las centrales hidroeléctricas con operación de tipo hydropeaking, inducen diariamente caudales artificiales y de corta duración en el río, los cuales ocurren cuando la demanda energética es máxima. Este tipo de operación provoca fuertes cambios en los caudales del río a escala diaria y horaria, con innumerables consecuencias ecológicas. En tanto, el esquema de operación de tipo run-of-river, utiliza el mismo caudal del río para generar energía y no tiene influencias significativas en las variaciones de caudal aguas abajo de la presa, en relación con el régimen de caudal natural del río en que operan (MacNaughton et al., 2015).

En cuanto al proceso de planificación territorial energético, para el desarrollo hidroeléctrico futuro en Chile, ha demostrado que una de las cuencas hidrográficas con mayor potencial hidroeléctrico es la del río Biobío. Esta cuenca brinda la posibilidad de generar aún 2.687 MW más de energía con la instalación de 191 centrales hidroeléctricas, aparte de las 11 centrales ya existentes. A ello se suma el potencial existente en las cuencas de los ríos Bueno (1.358 MW, con 179 centrales hidroeléctricas), Toltén (884 MW, con 144 centrales hidroeléctricas), e Imperial (455 MW, con 95 centrales hidroeléctricas), entre otras (Ministerio de Energía, 2016). La gran relevancia actual y futura de la energía hidroeléctrica para Chile, exige una mejora en nuestra comprensión sobre cómo la alteración del régimen de caudal por la operación de centrales modifica la funcionalidad de los distintos componentes de los ecosistemas acuáticos. Solo ello permitirá lograr el desarrollo de estrategias públicas de manejo y protección de caudales que satisfagan tanto las necesidades ecosistémicas, como la creciente demanda humana de agua y energía (Richter et al., 2003).

2.5 La importancia de la interacción del régimen de caudal y la geomorfología en los ecosistemas fluviales: brechas de conocimiento en el estudio de la alteración del régimen de caudales.

En la dinámica o en el ejercicio de comprender los efectos de la alteración del régimen de caudal en los ecosistemas fluviales, ha quedado en evidencia que el estudio de la sola regulación de caudales no siempre ha permitido entender los patrones ecológicos ni los cambios que se producen en los ecosistemas fluviales (Parsons et al., 2007; Meitzen et al., 2013). En variados estudios ha sido expuesta la complejidad de los sistemas acuáticos y cómo la interacción de diferentes elementos del sistema explica la variabilidad de los patrones ecológicos (Cowx et al., 2012; Jellyman et al., 2013). En este contexto se ha aceptado que la interacción de la hidrología con el hábitat físico de los ríos son los principales determinantes del carácter ecológico de los ríos (Southwood, 1977; 1988; Bunn & Arthington, 2002). Así, las comunidades ecológicas de los ecosistemas fluviales son el resultado de la interacción de ambos elementos (Walker et al., 1995; Poff et al, 1997; Ricther et al., 1998). En concreto, el régimen de caudal configura el carácter espacial y temporal de la geomorfología en ríos (Walker et al., 1995), y a su vez, el carácter físico de los ríos provee el espacio ("template") sobre el cual operan los procesos ecológicos y evolutivos (Southwood, 1977; 1978). De esta forma, tanto la hidrología y la geomorfología determinan la distribución, diversidad y abundancia de las comunidades biológicas en los ecosistemas fluviales (Schlosser 1982, Ward et al., 1999, Nilsson & Svedmark 2002). Es decir, ambos actúan como filtros para las especies, induciendo el incremento o disminución de algunos taxa subordinado directamente a sus rasgos funcionales (Poff et al., 2007; Carlisle et al., 2011). Así, influencian la abundancia de las distintas especies dependiendo de sus ciclos de vida, estrategias de desove (Montgomery et al. 1983, Nesler et al., 1988; Copp 1990), reclutamiento (Almodovar & Nicola, 1999), de alimentación (Troelstrup & Hergenrader, 1990), y tasas de crecimiento (Lagarrigue et al., 2002). Esta íntima relación entre las variables hidrológicas y geomorfológicas como desencadenantes de los patrones ecológicos hacen que la comprensión de los fenómenos de la ecología fluvial sea compleja y requiera del análisis integrado de estas dimensiones.

Aun cuando la importancia de la interacción de la geomorfología, hidrología y ecología, como también el rol activo y fundamental de estos dos primeros sobre la estructura de la fauna acuática de ríos ha sido identificada y reconocida por la ciencia fluvial, aún existen brechas de conocimientos acerca de su interacción. Ello dificulta la comprensión acabada de los efectos de la alteración hidrológica en los ecosistemas fluviales. En particular, desconocemos cómo el carácter geomorfológico de una cuenca fluvial influencia el nivel de impactos que una alteración hidrológica, pudiese ocasionar en términos ecológicos. Qué variables geomorfológicas son las que juegan el rol activo en la estructuración ecológica. Cuánto de la respuesta final de la biota es reflejo de la relación entre la geomorfología y la hidrología, y cuánto responde a la composición y "trade-offs" de rasgos intrínsecos de las especies que componen la comunidad.

2.6 Comprensión de los ecosistemas fluviales desde una perspectiva interdisciplinaria y jerárquica: un aporte a disminuir la brecha de conocimiento de los ecosistemas fluviales.

Los ríos son sistemas complejos, anidados y jerárquicos (Dólar et al., 2007; Thoms et al., 2007; Milner et al., 2016). Están constituidos estructuralmente, de parches bióticos e hidrogeomorfológicos que se encuentran organizados intrínsecamente de manera jerárquica y anidada. La jerarquía de estos parches puede descomponerse en distintos niveles de organización (Werner, 1999). Es así como, seis niveles de organización son reconocidos en geomorfología (cuenca, zonas de procesos funcionales, tramos de río, unidad funcional, mesohábitat y microhábitat) cuatro niveles jerárquicos temporales son reconocidos para la hidrología (régimen de caudal, historia de flujo, pulso de inundación e hidráulica del caudal) y cuatro niveles de organización son reconocidos para la ecología (ecosistema, comunidad, población e individuo; Thoms et al., 2002; Thorp et al., 2008; Meitzen et al., 2013). Bajo este contexto, el estudio apropiado de los sistemas fluviales, en cuanto a su estructura y funcionamiento, requiere necesariamente la vinculación de estos componentes (Montgomery, 1999; Thoms & Parsons, 2002 & Dólar et al., 2007).

Hemos enfatizado que la comprensión de la estructura y funcionamiento de un sistema fluvial natural o alterado no puede ser deducido del conocimiento de sus componentes individuales (Allen & Starr, 1982). Sino más bien, se requieren marcos y enfoques interdisciplinarios que integren cada componente del sistema fluvial y que garanticen la caracterización y evaluación de las redes fluviales a escalas apropiadas y acordes a las interrogantes formuladas. En este sentido, distintos modelos conceptuales propuestos (e.g. Vannote et al., 1980, Montgomery, 1999 Thorp et al., 2008) han sentado las bases para comprender y predecir las complejas interacciones y procesos que ocurren dentro de los sistemas fluviales. Thorp et al. (2008), en su libro "The Riverine Ecosystem Synthesis (RES)" proporciona un enfoque holístico para la clasificación de ríos. El RES propone que varios factores hidrogeomorfológicos, tales como el ancho de canal, sinuosidad de canal, ancho de valle, relación de ancho de canal a valle, precipitación, elevación y la geología pueden jugar un papel importante en la clasificación de los ríos y en la comprensión de los procesos y productos del ecosistema. Este modelo conceptual, es reconocido como un marco conceptual altamente explicativo de la estructura y el funcionamiento de los ecosistemas fluviales (Collins et al., 2014). En detalle, este modelo, describe la red fluvial como matrices de grandes segmentos hidrogeomórficos denominadas "Zonas de Procesos Funcionales" (FPZ, por sus siglas en inglés). Estas zonas se ubican en una escala espacial intermedia entre el valle y el tramo, y ocurren repetidamente a lo largo de la dimensión longitudinal de los ecosistemas fluviales (Thoms et al., 2004, Thoms et al., 2017). Constituyen unidades estructurales funcionales que acomodan procesos funcionales ecológicos y que describen procesos fluviales complejos que no están bien representados por secuencias lineales como las predichas por hipótesis tales como la del río continuo (Vannote et al. 1980). Las FPZs son descritas como zonas que permiten predecir la composición ecológica de las redes fluviales, ya que, sus atributos intrínsecos (ej. sedimentos, lecho del río, zonas de inundación) influyen en los rasgos y procesos ecológicos a través de las redes fluviales (estructura comunitaria y redes de alimentos; Masrii et al., 2019; Collins et al., 2014; Boys and Thoms 2006; Thoms et al., 2017). Por último, las FPZs son reconocidas como una escala apropiada para el manejo de estos ecosistemas (Thorp et al., 2010 y McCluney et al., 2014), ya que describen todas las variaciones hidrogeomórficas de la red hídrica, siendo cruciales para entender el funcionamiento de la red fluvial. En conclusión, las FPZ son una herramienta robusta para generar diseños de muestreo adecuados para responder preguntas sobre los efectos de las perturbaciones en los ríos, tanto en la estructura del río como en la biota acuática. Su distribución repetitiva a lo largo de los ecosistemas fluviales permite que se use para determinar los sitios de referencia dentro y entre las cuencas y, por lo tanto, para comparar adecuadamente la condición biológica de éstos (Chessman et al., 2004).

Por otro lado, en términos ecológicos, el nivel jerárquico utilizado para monitorear cambios ambientales debe estar acorde con la escala en que los procesos físicos e hidrológicos observados ocurren (Allen & Hoekstra, 1990). Así también, es importante considerar el grupo biótico que se utilizará como indicador de las respuestas ecológicas al cambio ambiental. En este sentido, los peces y macroinvertebrados son excelentes indicadores de la estructura y funcionamiento de los ecosistemas fluviales (Dos Santos et al., 2011; Fierro et al., 2015). Ambos son reconocidos como indicadores capaces de integrar y reflejar acumulativos cambios a lo largo del tiempo (Fierro et al., 2015). Por lo demás, una ventaja notable de usar estos grupos bióticos es la relativa simplicidad de su captura y muestreo. Por otro lado, la integración de respuestas de ambos grupos en un análisis ambiental permite el reconocimiento de respuestas que no podrían ser observadas en un análisis individual. Esto sin duda alguna, robustece nuestra comprensión de los efectos de los cambios ambientales en los distintos componentes de los sistemas fluviales.

2.7 Las cuencas de los ríos Biobío e Imperial como modelos de estudio.

Uno de los objetivos principales de esta investigación es evaluar, a escala espacial de zona de proceso funcional, en qué medida la estructura de ensambles de macroinvertebrados y peces se ve afectada por la regulación de caudales. Mediante el uso del marco teórico proporcionado por RES, realizamos un estudio que abarca las respuestas ecológicas de dos grupos bióticos - desde una perspectiva espacial de macro-escala (FPZs) - a distintos gradientes de perturbación hidrológica. Para ello, esta investigación se desarrolló utilizando como modelos de estudio dos hoyas hidrográficas con distintos grados de alteración hidrológica, las cuencas del río Biobío y río Imperial. La cuenca del río Biobío es la hoya hidrográfica con mayor diversidad de especies de peces en Chile (24 especies; Vila & Habit, 2015) y la tercera más grande del país. Hoy en día, su caudal se encuentra ampliamente intervenido por 11 grandes centrales hidroeléctricas, con distintos tipos de operación, tales como hydropeaking y run-of-river, instaladas tanto en su cauce principal como en sus tributarios. Para abordar los objetivos de esta investigación que consisten en evaluar zonas con caudal natural e intervenido, propusimos la búsqueda de zonas de referencia, en términos hidrológicos, en una cuenca sin alteración hidrológica como es la cuenca del río Imperial. La elección de esta cuenca como una cuenca de referencia se basó en una evaluación de las características ambientales y ecológicas. En este sentido, se reconoció que ambas cuencas están localizadas a similar latitud, 36° y 39° en el caso de la cuenca del río Biobío y entre 37° y 38° la del río Imperial. Ambas cuencas, se originan en la Cordillera de los Andes, una a 1500 m.s.n.m (cuenca río Biobío) y otra a 1400 m.s.n.m (cuenca río Imperial). Poseen un clima templado con influencia mediterránea, con precipitaciones del orden de 1200 a 4000 mm al año y con un hidrograma de descarga diaria similar en su desembocadura (Figure 2.2). En términos de calidad de agua, ambos ríos exhiben aguas oligotróficas, caracterizadas por bajas concentraciones de nutrientes (fósforo y nitrógeno), bajas concentraciones de solidos suspendidos, conductividad menor que 120 µS y según su pH son consideradas aguas neutras a ligeramente alcalinas (Faranda & Parra, 1993; DGA, 2004). En términos ecológicos, presentan una alta similitud en composición ictiofaunística y de invertebrados bentónicos, debido a que tanto la cuenca del río Biobío como la del río Imperial se encuentran ubicadas dentro de una misma área ictiogeográfica y *hotspot* de biodiversidad de invertebrados de agua dulce, la Provincia Chilena, área de endemismo centro-sur (Dyer, 2000; Valdovinos, 2008). La comunidad de peces en la cuenca del río Biobío está compuesta de 18 especies nativas y 5 no nativas (Vila & Habit, 2015; Tabla 2.2). Mientras que en la cuenca del río Imperial son reconocidas 15 especies nativas y 5 no nativas. La comunidad de macroinvertebrados bentónicos está compuesta principalmente por estados inmaduros de insectos acuáticos (Valdovinos & Parra, 2006). Entre los órdenes dominantes se encuentran Plecoptera, Diptera, Trichoptera, Ephemeroptera y Coleoptera.

Cabe destacar, que la comparación de ambas cuencas, realizada a escala de zonas de procesos funcionales, se basa en la premisa que una zona de proceso funcional posee la extensión espacial apropiada para capturar la variabilidad del caudal y que, además, una misma zona de procesos funcional, localizada en distintas áreas de la cuenca y entre cuencas presenta características funcionales y estructurales similares.

Tabla 2.2. Lista de especies de peces presentes en la cuenca de los ríos Biobío e Imperial (basado en Vila et al., 1999; Dyer, 2000; Vila & Habit, 2015).

Origen	**Especies**	**Cuenca río Biobío**	**Cuenca río Imperial**
Nativos	*Aplochiton zebra (Jenyns, 1842)*	X	
	Basilichthys microlepidotus (Jenyns, 1842)	X	X
	Brachygalaxias bullocki (Regan, 1908)	X	X
	*Bullockia maldonadoi (*Eigenmann, 1920*)*	X	X
	*Cheirodon galusdae (*Eigenmann, 1927*)*	X	X
	Diplomystes nahuelbutaensis (Arratia, 1987)	X	X
	Geotria australis (Gray, 1851)	X	X
	Galaxias maculatus (Jenyns, 1842)	X	X
	Mordacia lapicida (Gray, 1851)	X	X
	Nematogenys inermis (Guichenot 1848)	X	X
	Odontesthes mauleanum (Steindachner, 1896)	X	X
	Odontesthes brevianalis (Günther 1880)	X	X
	Percilia irwini (Eigenmann, 1927)	X	
	Percilia gillissi (Girard, 1854)		X
	Percichthys trucha (Valenciennes, 1833)	X	X
	Percichthys melanops (Valenciennes, 1833)	X	X
	Trichomycterus areolatus (Valenciennes, 1848)	X	X
	Trichomycterus chiltoni (Eigenmann, 1927)	X	
No nativos	*Cyprinus carpio (Linnaeus, 1758)*	X	X
	Carassius carassius (Linnaeus, 1758)	X	X
	Gambusia holbrooki (Girard, 1859)	X	X
	Oncorhynchus mykiss (Walbaum 1792)	X	X
	Salmo trutta (Linnaeus, 1758)	X	X

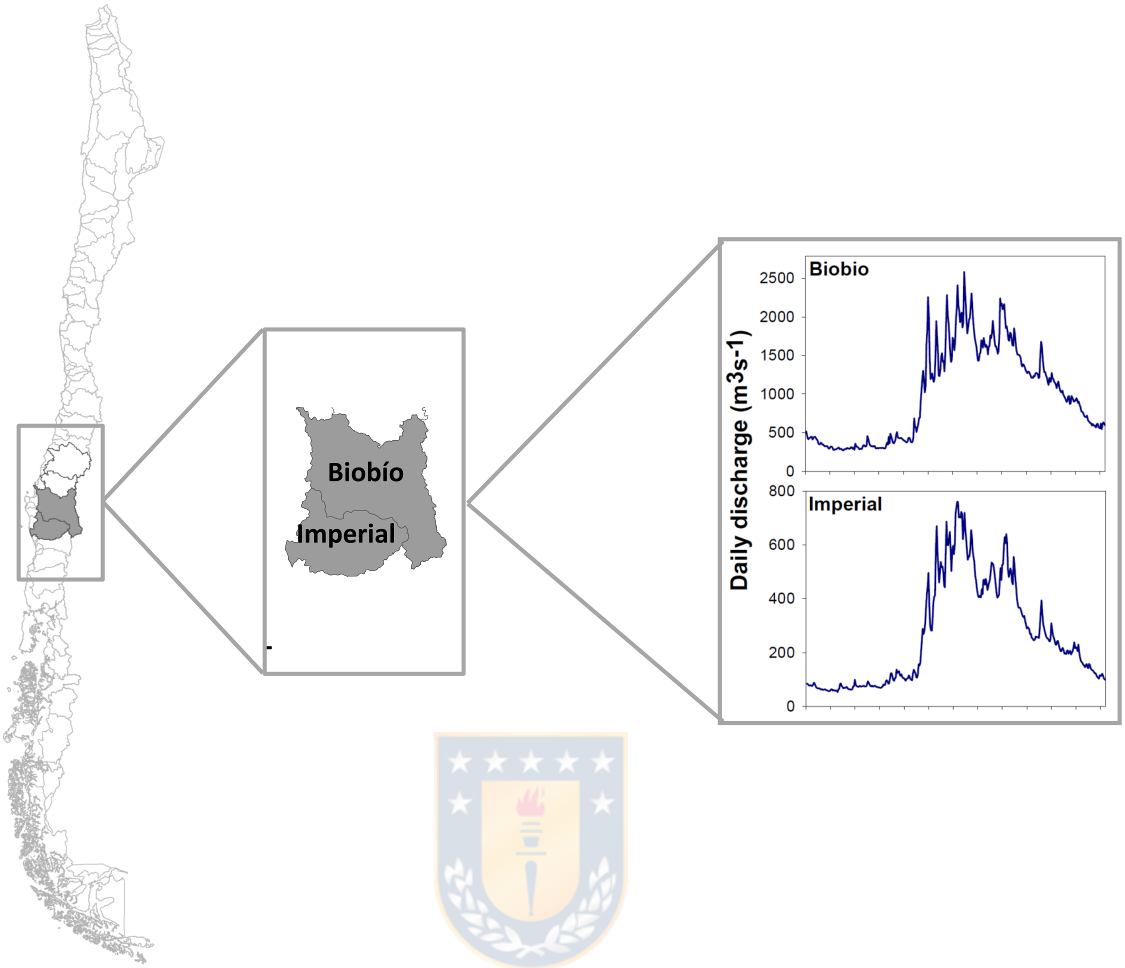

Figure 2.2. Ubicación geográfica e hidrograma anual de las cuencas de los ríos Biobío e Imperial.

3 HIPÓTESIS.

El régimen de caudal actúa como el principal filtro ambiental de especies en los sistemas fluviales, por lo cual, las alteraciones que ocurren en él implican cambios en la composición y estructura taxonómica y funcional de la biota acuática. En esta investigación se plantea que las centrales hidroeléctricas instaladas en la cuenca del río Biobío, generan efectos adversos sobre las comunidades de macroinvertebrados y peces, los que dependen del tipo y magnitud de la alteración del régimen de caudal y de la zona de proceso funcional del río donde ocurre la modificación de caudal. En este sentido, se espera que se cumplan las siguientes predicciones:

- La distribución de las comunidades de macroinvertebrados y peces difieren entre las distintas zonas de procesos funcionales.
- Las principales alteraciones del caudal serán producto de centrales hidroeléctricas con operación de tipo *hydropeaking*.
- Las respuestas a la regulación de caudal de las comunidades y especies de ambos grupos biológicos serán mediadas por las características intrínsecas de las zonas de procesos funcionales.
- Los mayores efectos en la comunidad de macroinvertebrados y peces, en cuanto a su abundancia, ocurrirá en aquellas FPZs donde son más abundantes.
- Los macroinvertebrados con rasgos funcionales de alimentación, tales como, trituradores y filtradores reducirán sus abundancias significativamente en secciones de río con alteración hidrológica.
- Peces que habitan columna de agua presentarán mayores cambios a la alteración hidrológica que aquellos de hábitos bentónicos.
- Variables hidrológicas a escala de tiempo corto (sub-diaria) y variables geomorfológicas a escala espacial pequeña (canal), serán aquellas que explican la configuración y respuestas de la estructura de ensambles de macroinvertebrados y peces.

4 OBJETIVOS

4.1 Objetivo General

El objetivo de esta investigación fue determinar el rol de la interacción entre la geomorfología y la hidrología en la determinación de los cambios en la composición taxonómica y funcional de comunidades de macroinvertebrados y peces. Para ello se estudiaron las alteraciones del régimen de caudal de tipo hydropeaking y run-of-river y sus efectos en la composición, diversidad y distribución espacial de atributos taxonómicos y funcionales de macroinvertebrados y peces en distintas zonas de procesos funcionales.

4.2 Objetivos específicos

1. Determinar y describir las características de las zonas de procesos funcionales presentes en los ríos Biobío e Imperial.

2. Describir todos los componentes del régimen de caudal, reconociendo zonas de procesos funcionales con régimen de caudal natural y régimen de caudal alterado.

3. Determinar las respuestas de los atributos funcionales y taxonómicos de comunidades de macroinvertebrados y peces en zonas de procesos funcionales con diferente tipo de alteración del régimen de caudal.

4. Determinar las principales variables geomorfológicas e hidrológicas que determinan las respuestas de los ensambles de macroinvertebrados y peces, así como las escalas espaciales a las que operan.

5 CAPITULO I. FUNCTIONAL PROCESS ZONES AND THEIR FISH COMMUNITIES IN TEMPERATE ANDEAN RIVER NETWORKS.

Este capítulo está basado en:

Anaysa Elgueta, Martin Thoms, Konrad Górski, Gustavo Díaz & Evelyn Habit. 2019. Functional process zones and their fish communities in temperate Andean river networks. River research and applications.

5.1 Introduction

Understanding how the physical structure of river networks determines ecological conditions, thus biological communities are critical for conserving species, monitoring and assessment, understanding potential anthropogenic influences, and achieving desired targets for the ecosystem sustainability of river ecosystems (Dollar, James, Rogers, & Thoms, 2007; Gilvear, Greenwood, Thoms, & Wood, 2016). Physical and biological components that interact within riverine ecosystems generate distinct spatial patterns that can be observed at multiple scales (Thoms, Delong, Flotemersch, & Collins, 2017). The physical and ecological structures of river networks display these interactions as simple continuous downstream gradients (cf. the River Continuum Concept of Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) or a mosaic of river zones that differ in length, physical composition, and spatial arrangement (Thorp, Thoms, & Delong, 2008). The spatial pattern of biophysical character reflects variations in hydrological and sediment regimes and valley conditions throughout a river network as well as a myriad of physical–ecological feedbacks. Examples of more complex spatial interactions include the concept of Process Domains (Montgomery, 1999) and the Riverine Ecosystem Synthesis of Thorp, Thoms, and Delong (2006). The Riverine Ecosystem Synthesis portrays river networks as a series of river zones termed functional process zones (FPZs). Different FPZs have been shown to have different riverbed habitats (Collins, Thoms, & Flotemersch, 2014) and food web character (Thoms et al., 2017).

A shift in the study and management of riverine landscapes from site/local reach-based approaches to a larger catchment scale has occurred since the early 2000s (Thoms, Gilvear, Wood, & Greenwood, 2016). River scientists are often challenged to detect and quantify the drivers of ecosystem response, including interactions and feedbacks, at large scales. Although there are many traditional approaches to river research, monitoring, and assessment, they are generally limited to reach or site scales (Milner, Gilvear, & Thoms, 2016). Commonly, data collected at the reach scale are upscaled and used to characterize and assess entire river networks. The hierarchical nature of river systems and the principles of hierarchy theory suggest this is scientifically inappropriate (Dollar et al., 2007). River systems display unique and emergent properties relevant to the scale of analysis. Hence, the structure and function at higher levels of organization (e.g., entire river networks) cannot be obtained from the summation of individual components at lower levels of organization (e.g., individual reaches; Allen & Starr, 1982; Thoms, Scown, & Flotemersch, 2018).

The study and management of entire river networks demand data, information, and tools to be applied at appropriate spatial scales. FPZs possess intrinsic physical attributes influencing ecological traits both within and across river networks (Thorp et al., 2008). The ability to identify the form, function, arrangement, and location of FPZs may provide a means to predict the ecological composition of river networks a priori. In addition, FPZs have been suggested as the appropriate scale for river management as they describe variations in geomorphology and ecology of a river network (Thorp et al., 2008). Knowledge of character, distribution, arrangement, and function of FPZs in a river network may allow prediction of the distribution and community structure of riverine biota. Furthermore, it can aid in the development of sampling designs that address the effects of anthropogenic disturbances by comparisons of disturbed and reference sites within the same FPZ. Some tools are available to characterize FPZs and river networks, for example, NetMap that provides numerous functions for calculating watershed attributes (Benda et al., 2007). Available high-resolution digital elevation model data and accessible top-down techniques allow identification of FPZs within a river network (Thoms, Rayburg, & Neave, 2007; Williams et al., 2013). These techniques may improve conceptual understanding of river systems from an ecogeomorphological perspective and inform river management and conservation activities (Gilvear et al., 2016).

Fish are excellent indicators of the ecological status of river networks as they often require a wide range of riverine conditions over their life cycle, from properties of bed sediments for egg development to longitudinal integrity for spawning migrations

(Schiemer, 2000). Furthermore, fish distribution and abundance are strongly related with physical habitat characteristics at microhabitat scale (Gorman & Karr, 1978). Sampling programmes that aim to assess the status of rivers at the network scale would strongly benefit if fish–habitat relationships can be upscaled to the FPZ level. However, this may only be possible if similar fish communities can be identified within of the same FPZs across river networks.

Andean rivers in Chile serve as an excellent model to evaluate fish community–FPZ relationships. These river systems are relatively short (<440 km) and characterized by a range of elevations across basins so expected to accommodate a diversity of FPZs. They drain from east to west and form a collective of parallel basins distributed along a latitudinal gradient (Campos, 1985; Marin, Delgado, & Vila, 2006) that experience multiple natural and anthropogenic stressors (Aguayo, Pauchard, Azocar, & Parra, 2009). Increasingly, dams and the generation of hydroelectric power, land use changes, water extractions for irrigation, industrial, and domestic effluents are having a significant effect on these systems (Habit et al., 2019). Differences in latitudinal position and anthropogenic impact make it difficult to develop suitable sampling designs that would reveal cause–effect relationships between anthropogenic activities and biotic changes. Fish communities in Chilean Andean rivers are characterized by high level of endemism and have undergone significant changes in response to anthropogenic impacts in recent decades. Knowledge of FPZs potentially provides key information for designing appropriate sampling for efficient monitoring at river network scale that is essential to inform conservation of this highly unique and threatened fish fauna.

In this study, we assess the spatial arrangement of FPZs within two contiguous river basins of central-southern Chile (the Biobío and Imperial Rivers) using a series of automated geographic information system tools. We examine the structure and occurrence of FPZs in the Biobío and Imperial Rivers (i.e., frequency, distribution, and diversity). Subsequently, we investigate the association between FPZs and fish assembages in the Biobío River network. We expect that specific fish assemblage inhabits each FPZ within a river network and reflects its character.

5.2 Study Area

This study was conducted in the Biobío and Imperial river networks in Central Chile (Figure 5.1). Chilean freshwater ecosystems have a conservation priority because of extremely high levels of faunal endemism (e.g., 82% of the fish species; Vila & Habit, 2015). Moreover, central Chile is considered to be a global biodiversity hotspot (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). In terms of freshwater fish fauna, the Biobío River is the most species-rich river in Chile and is inhabited by 18 native species that represent 39% of all Chilean fish species. Two of these species (darter, *Percilia irwini*; and catfish, *Trichomycterus chiltoni*) are endemic to the basin. The fish fauna of adjacent Imperial River is similar and accommodates 15 native species.

The Biobío River has a catchment area of 24,029 km^2 and is located between 36° and 39° latitude south. It originates in the high Andes (1500 m above sea level), travels in an east–west direction for 407 km before flowing into the Pacific Ocean and has mean annual discharge of ~900 $m^3 s^{-1}$ in its lowest reaches (Niemeyer & Cereceda, 1984). The Imperial River Basin, by comparison, extends between 37° and 38° latitude south and has a catchment area of 12,054 km^2. This river also originates in the high Andes (1400 m above sea level), has a total length of 230 km, and mean annual discharge of 240 $m^3 s^{-1}$ in its lower most reaches (Niemeyer & Cereceda, 1984). The climate of both rivers is wet–temperate with a Mediterranean influence, and annual rainfall varies from 1,200 to 4,000 mm. As a result, flows in both rivers are generally higher between the months of July and November (austral winter and spring). Both river networks are considered to be highly vulnerability to climate change because of projected temperature increases and decreases of rainfall in coming decades (Intergovernmental Panel for Climate Change, 2015).

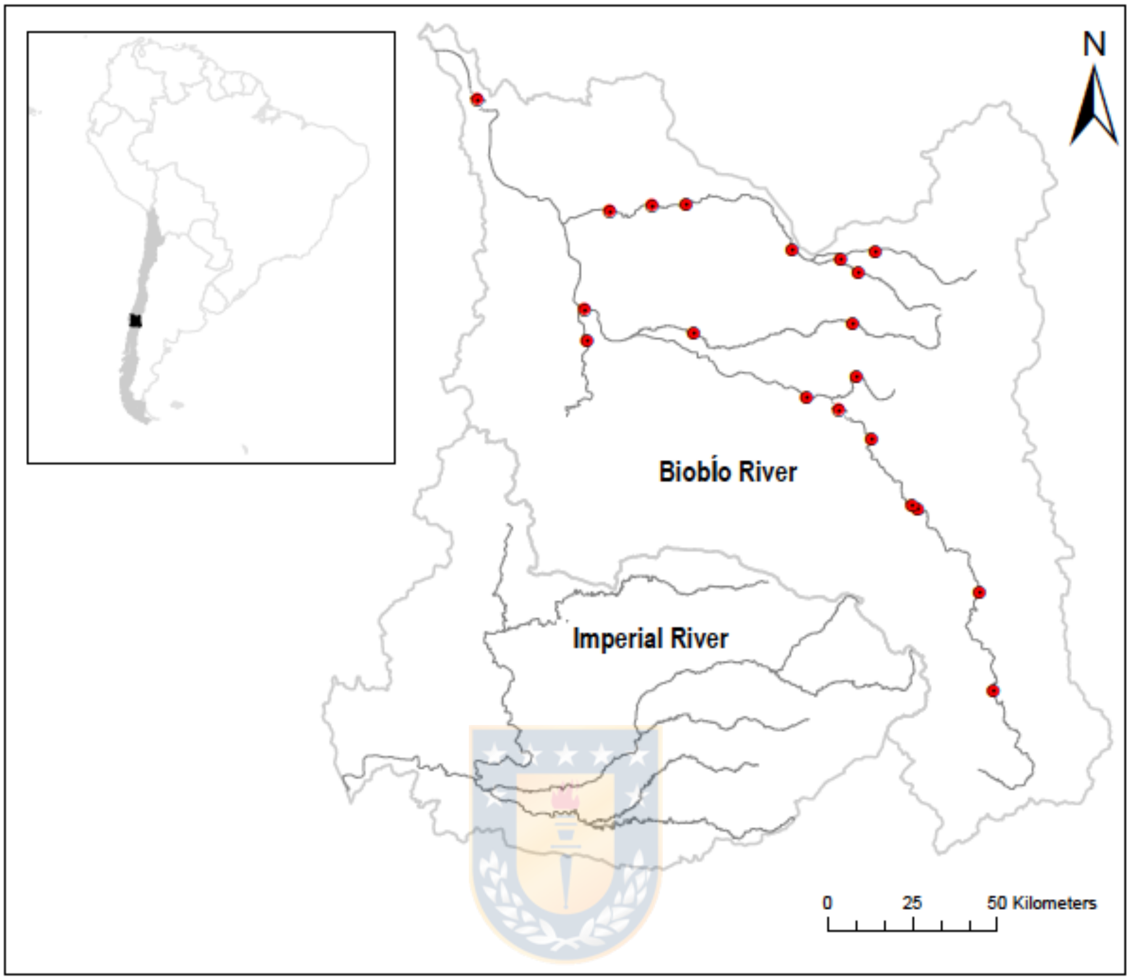

Figure 5.1. The Biobío and Imperial Rivers and their location in South America. Fish sampling sites are indicated in the Biobío River.

5.3 Methods

5.3.1 Data sources

The river networks of the Biobío and Imperial rivers were obtained from the Chilean National Hydrography data set, which provides a 1:50.000-scale digital representation. The river network of each system was divided into 5-km reaches following the approach recommended by Thoms et al. (2018). Each reach defined a site, and 160 sites were defined in the Biobío River and 187 in Imperial River. At each site, 15 variables were extracted to characterize the hydrogeomorphological character (Table 5.1). Variables were measured at three spatial scales (catchment, valley, and channel) using a series of ArcGIS tools (Williams, D'Amico, Kastens, et al., 2013). Catchment-scale variables were elevation, geology, and rainfall. Elevation was determined from a 30-m digital elevation model obtained from Shuttle Radar Topography Mission, National Aeronautics and Space Administration, USA. Mean long-term annual rainfall was derived from raster data sourced from the Chilean Water Division (DGA). Geology was measured from a 1:1,000,000-scale vector geology map of the catchment (Servicio Nacional de Geología y Minería, 2003) and aggregated into three basic categories and ranked on the basis of their basic sediment transport process and potential sediment: colluvial, alluvial, and fluvial. Valley scale variables were valley width, valley trough width, the ratio of valley width to the valley trough width, the left and right valley slopes, down valley slope, and valley confinement (see Figure 5.6; Harris, Thoms, Rayburg, & Parsons, 2008). The channel-scale variables were channel belt width, channel belt sinuosity, channel belt wavelength, as well as river channel sinuosity, planform, and the number of river channels.

Table 5.1. Geomorphological variables used for determination of functional process zones.

Scale	**Geomorphic variables**	**Unit**	**Data Source**
Catchment	Elevation	m	30m DEM of catchment
Catchment	Geology: sediment process and potential yield	DL	Chile geological map 1:1,000,00
Catchment	Mean annual rainfall	mm	National rainfall map of Chile
Valley	Valley width	m	30m DEM of catchment
Valley	Valley trough width	m	30m DEM of catchment
Valley	Ratio of valley to valley trough width	m	30m DEM of catchment
Valley	Left valley slope	DL	30m DEM of catchment
Valley	Right valley slope	DL	30m DEM of catchment

Scale	Geomorphic variables	Unit	Data Source
Valley	Down valley slope	DL	30m DEM of catchment
Valley	Confinement	DL	30m DEM of catchment
River Channel	Channel belt wavelength	m	River polygon
River Channel	Channel belt sinuosity	DL	River polygon
River Channel	Channel belt width	m	River polygon
River Channel	Number of channels	DL	River polygon
River Channel	River sinuosity	DL	River polygon

Note. m, metres, mm, millimetres, and DL, dimensionless. Abbreviation: DEM, digital elevation model.

5.3.2 Assessment of Functional Process Zones

To identify groups of river reaches with similar hydro-geomorphological character (FPZs), a variety of multivariate statistical techniques was used. Data obtained for each river network were analyzed together to allow emergence of FPZs similar across the two networks. First, hierarchical cluster analysis was performed using unweighted pair-group method with arithmetic averages algorithm. This method was selected because of its high suitability for groupings on the basis of environmental variables of different character (Belbin & McDonald, 1993; Legendre & Birks, 2012), although different clustering techniques may yield different results. Clustering was based on the Gower association measure because this measure is range standardized and is recommended for nonbiological data (Belbin, 1993). On the basis of the results of cluster analysis, groups of reaches were selected. The criterion of selection was based on the inflexion point in the curve of relationship between the number of groups in the cluster and their corresponding similarity value (Thoms et al., 2018). Once identified, similar groups were arrayed onto the streamlines of the Biobío and Imperial Rivers to delineate the position of reaches with similar morphological character. Groups of sites with similar morphological character equate to FPZs. To determine significant differences among FPZs a permutational multivariate analysis of variance on the basis of the Gower association matrix was performed (Anderson, 2014). A similarity percentage (SIMPER) analysis was then undertaken to determine which geomorphic variables contributed most to the within-group similarity of each FPZ (Clarke, Somerfield, Airoldi, & Warwick, 2006). The results of this analysis were used to construct an FPZ nomenclature for river networks of the Biobío and Imperial. The number of sites assessed varied among FPZs and ranged between 3 and 30 depending on their extension within the river network. In addition, during field surveys conducted to confirm the presence of FPZ, the dominant riverbed sediment texture was identified within each FPZ. Consequently, riverbed substratum types (i.e., boulders, cobbles, pebbles, gravel, sand, or silt) were also included in the descriptions of each of the FPZ.

To assess the organization and singularity of each FPZ within river networks, diversity metrics were used (Thoms et al., 2018). The river networks were recognized as a community of FPZs, where a “functional process zone (FPZ)” is analogous to a “species” in ecology. Diversity of each FPZ was measured at the whole-network scale using Shannon–Weiner diversity index (H), where H′ is

$$H' = -\sum p_i \ln p_i$$

and pi is the proportion of reach lengths found in the ith FPZ in each stream of the river network. Richness was calculated as the number of FPZs present in the network and abundance as the total length of the river network of each FPZ.

5.3.3 Relation of FPZ and fish communities

Fish abundance data collected during water quality monitoring campaigns performed by the EULA Centre of the University of Concepción, Chile, were available only for the Biobío River. A total of 20 sites were sampled within the river network between 2016 and 2019. On the basis of their geographic coordinates, each monitoring site was assigned to one of the identified FPZs. Fish obtained during these monitoring campaigns were sampled using electrofisher (Halltech), beach seine (10 m long and

1.5 m high and mesh size = 6 mm), and Nordic standard gillnets in reservoirs (30 m long and 1.5 m high and mesh size = 29 mm). These data were used to identify whether each of the specific FPZ is characterized by a particular fish community. The relative abundance of each species was estimated by FPZ using all sites within each FPZ. Differences among FPZs were compared using analysis of similarities (Clarke & Warwick, 2006). Subsequently, species with the highest contribution to differences among FPZ were identified using SIMPER analysis (Clarke & Warwick, 2006). Both analyses were performed on the basis of standardized and square root-transformed abundance data (Clarke & Warwick, 2006).

5.4 Results

5.4.1 Composition and organization of FPZs.

Seven FPZs emerged from the statistical analysis of the 347 reach segments in the Biobío and Imperial river networks (Figure 5.2). The cluster analysis (Figure 5.2) showed a clear separation of similar groups of sites, and this explained 71% of the similarity between all sites (Figure 5.2). Each FPZ was significantly different to one another in terms of its physical character (permutational multivariate analysis of variance, Pseudo- F (6) = 33.17, p = .0001, Nperm = 9999; Figure 5.3). The SIMPER and the field data allowed for naming of the seven FPZs (cf. Figure 5.2). Upland regions (Andean, Sub-Andean, and Reservoir) are characterized by higher downstream slopes, colluvial and fluvial sediments, and narrower valley widths and are generally located in the upper or headwater regions of the catchment (Figure 5.2 and Figure 5.3). Channel planform separated reservoirs from Sub-Andean FPZ. Central Valley region contained “Central Valley Cobble Dominated” and “Central Valley Gravel Dominated” FPZs (Figure 5.2). This is a region of lower relief, lower slopes, and with wider valley floors and floodplains. The distinction between these two FPZs is one influenced by volcanic activity hence a large riverbed sediment texture—cobble versus gravel bed (Figure 5.3). The tortuous alluvial FPZ was the only FPZ characterized by meandering channels (Figure 5.2 and Figure 5.3). The lowland FPZ has distinctly wider valley floors hence the presence of floodplains and lower slopes; thus, rivers in this FPZ display characteristic sinuous river channel planforms and riverbed sediments dominated by fine sands (Figure 5.3).

Overall, four FPZs were shared between the Biobío and Imperial networks (Figure 5.2); these were the Sub-Andean, Central Valley Cobble Dominated, Central Valley Gravel Dominated, and the lowland FPZ. Of the three remaining FPZs, two were only found in the Biobío River (Andean and reservoir) and one was unique to the Imperial River (tortuous alluvial; Figure 5.2). In general, the FPZs were spatially distributed in discrete areas of the river network. However, some FPZs repeated themselves along the river network (Figure 5.2). Transitions between FPZ types were not orderly in the downstream direction. The Central Valley cobble dominated FPZ most frequently transitioned into the Central Valley gravel dominated FPZ (n = 15) and vice versa (n = 9), whereas the Sub-Andean transitioned into the Central Valley Cobble Dominated less frequently (n = 7). Both Central Valley FPZs transitioned to the Lowland FPZ; this occurred seven times for Central Valley Gravel Dominated FPZ and one time for Central Valley Cobble Dominated FPZ. The variation in the number of types of FPZ transitions indicates a nonclinal downstream organization of channel morphologies in these river networks.

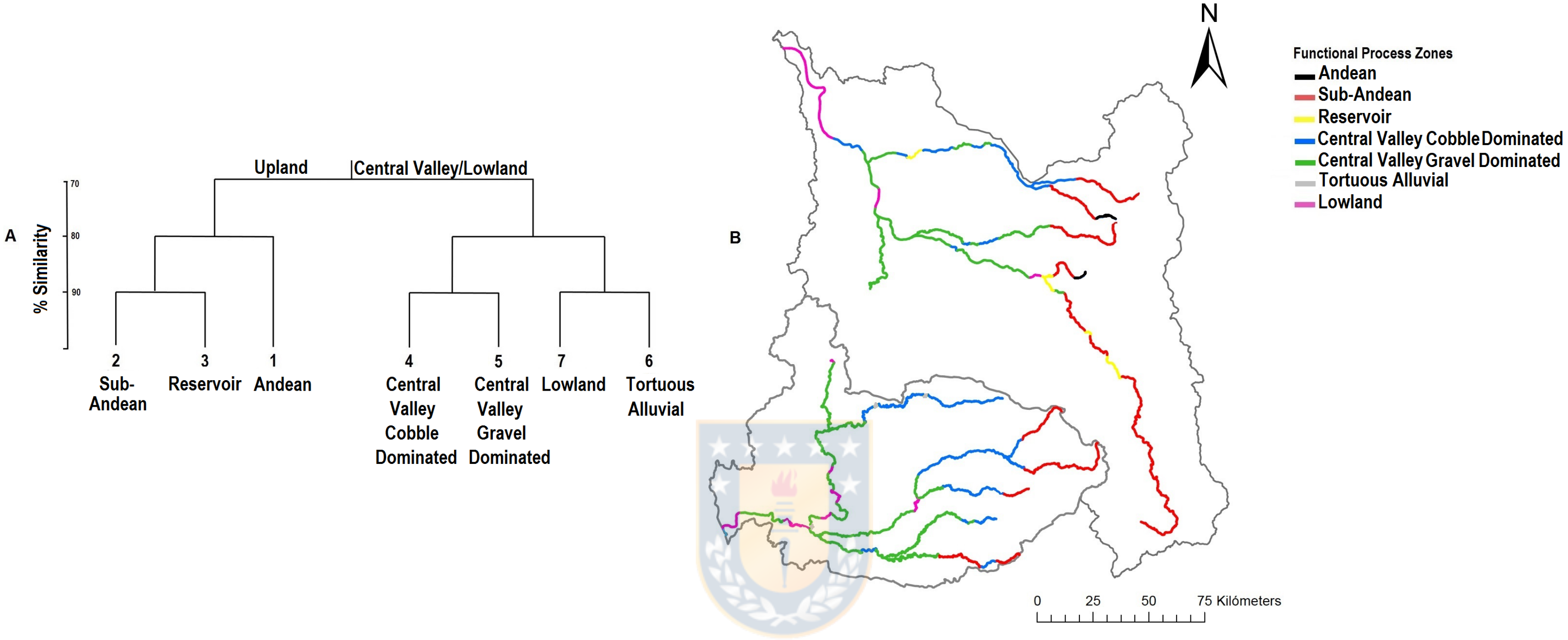

Figure 5.2. The functional process zones of the Biobío and Imperial Rivers. (a) The classification dendrogram and (b) spatial organization of functional process zones within the Biobío and Imperial river networks

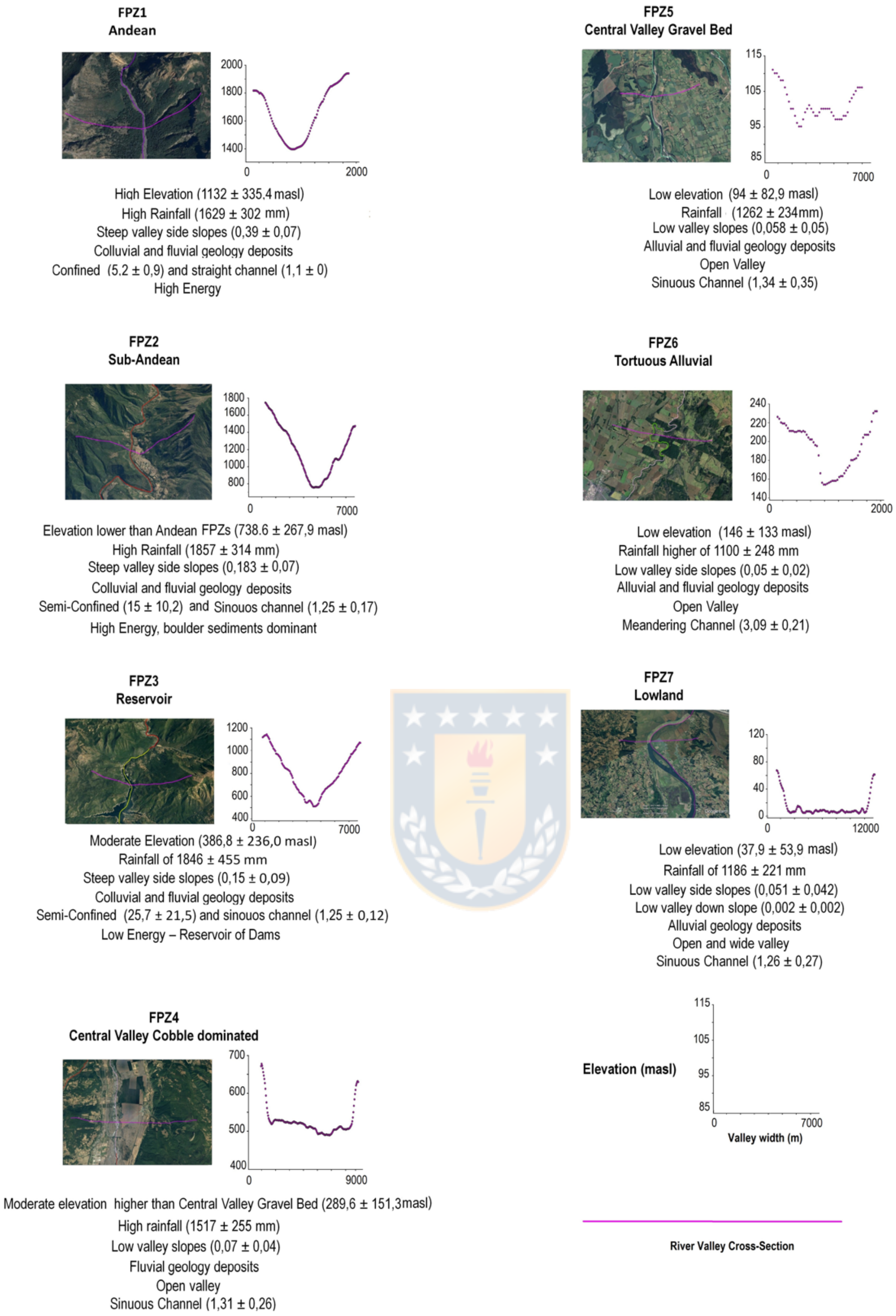

Figure 5.3. Main character of the functional process zones. These characteristics were based on the SIMPER analysis (percentage of contribution of each variable to the functional process zones association).

5.4.2 Composition and diversity of FPZs.

The composition and diversity of the FPZs within the Biobío and Imperial river networks varied in terms of the abundance and richness of individual segments comprising each FPZ (Figure 4). Overall, the diversity of FPZs in the Biobío River (mean Shannon diversity of 1.47) was higher than in the Imperial River (mean Shannon diversity of 1.27). The diversity of individual FPZs also varied between the two river networks (Figure 4). The most diverse FPZs in both rivers were FPZs located in the Central Valley region (Figure 4). Sub-Andean and Lowland FPZs showed contrasting patterns between the two rivers, where Sub-Andean was more diverse in the Biobío River and Lowland in the Imperial River.

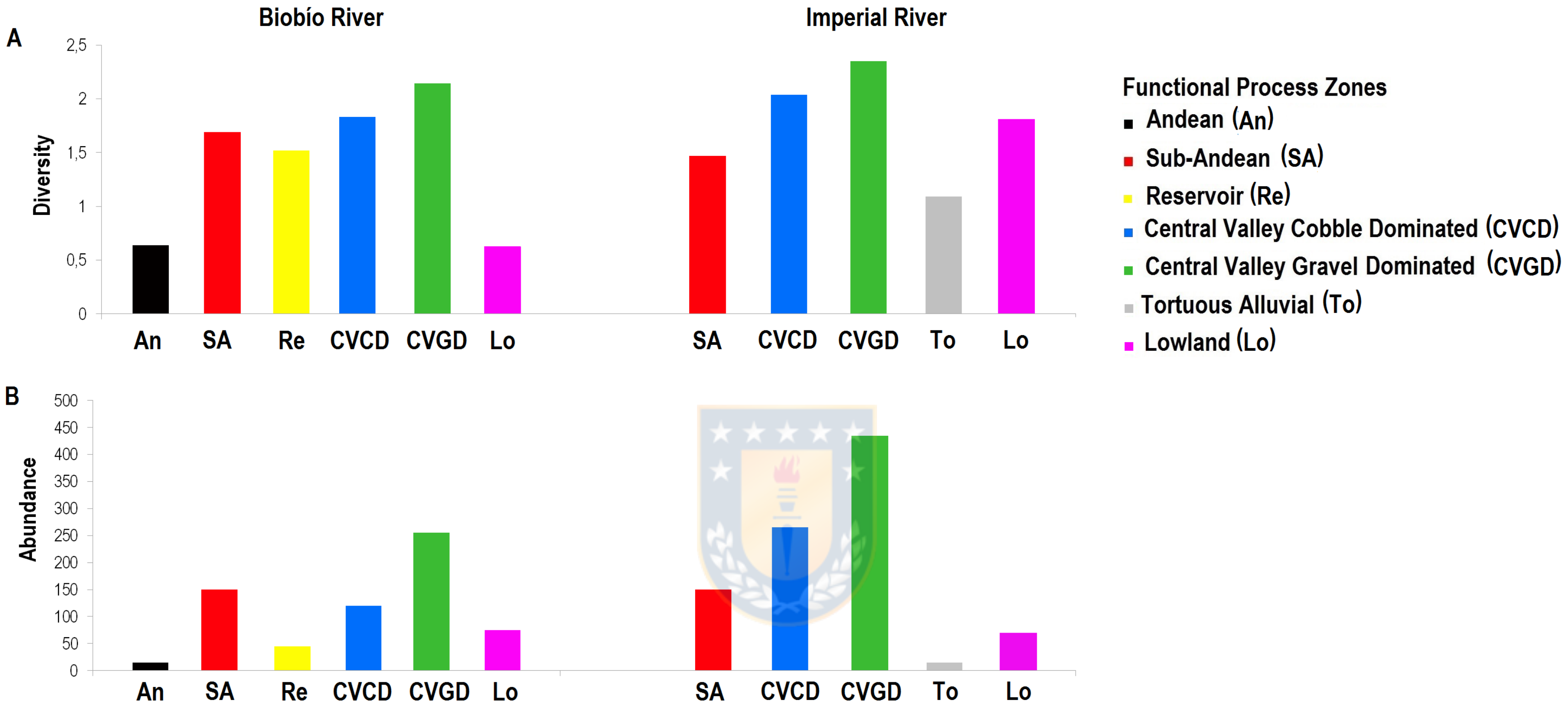

Figure 5.4. Diversity of each functional process zone (a) and abundance of reaches within each functional process zone (b) identified in the Biobío and Imperial river networks. Nonnative species indicated with asterisk.

5.4.3 *Fish community in each FPZ*

The number of fish monitoring sites in the Biobío River differed among FPZs and generally more abundant FPZs were sampled more frequently (Figure 5.1). A total of nine native and six nonnative fish species were collected in the Biobío River during campaigns between 2016 and 2019 (Table 5.2). Each FPZ was inhabited by a specific fish community (analysis of similarities, R = .358, p = 0.001; Figure 5.5; Table 5.3). Nonnative rainbow and brown trout were abundant in Sub-Andean FPZ associated with high energy and low water temperatures. Reservoirs were dominated by native pelagic perch (*Percichthys trucha*) and nonnative rainbow trout (*Oncorhynchus mykiss*). Both Central Valley FPZs were characterized by high abundances of native open water darter (*P. irwini*) and benthic catfish (*Trichomycterus areolatus*; Figure 5.5). In addition, Central Valley Cobble Dominated FPZ that is located at mid elevations and is characterized by coarse substrate had higher species richness and presence of nonnative open water rainbow trout and mosquitofish (*Gambusia holbrooki*). In contrast, native open water perch and silverside (*Basilichthys microlepidotus*) as well as puye (*Galaxias maculatus*) were also abundant in the Central Valley Gravel Dominated FPZ (Figure 5). Lowland FPZ was dominated by native open water silverside, darter, and puye in addition to nonnative open water mosquitofish (Figure 5.5).

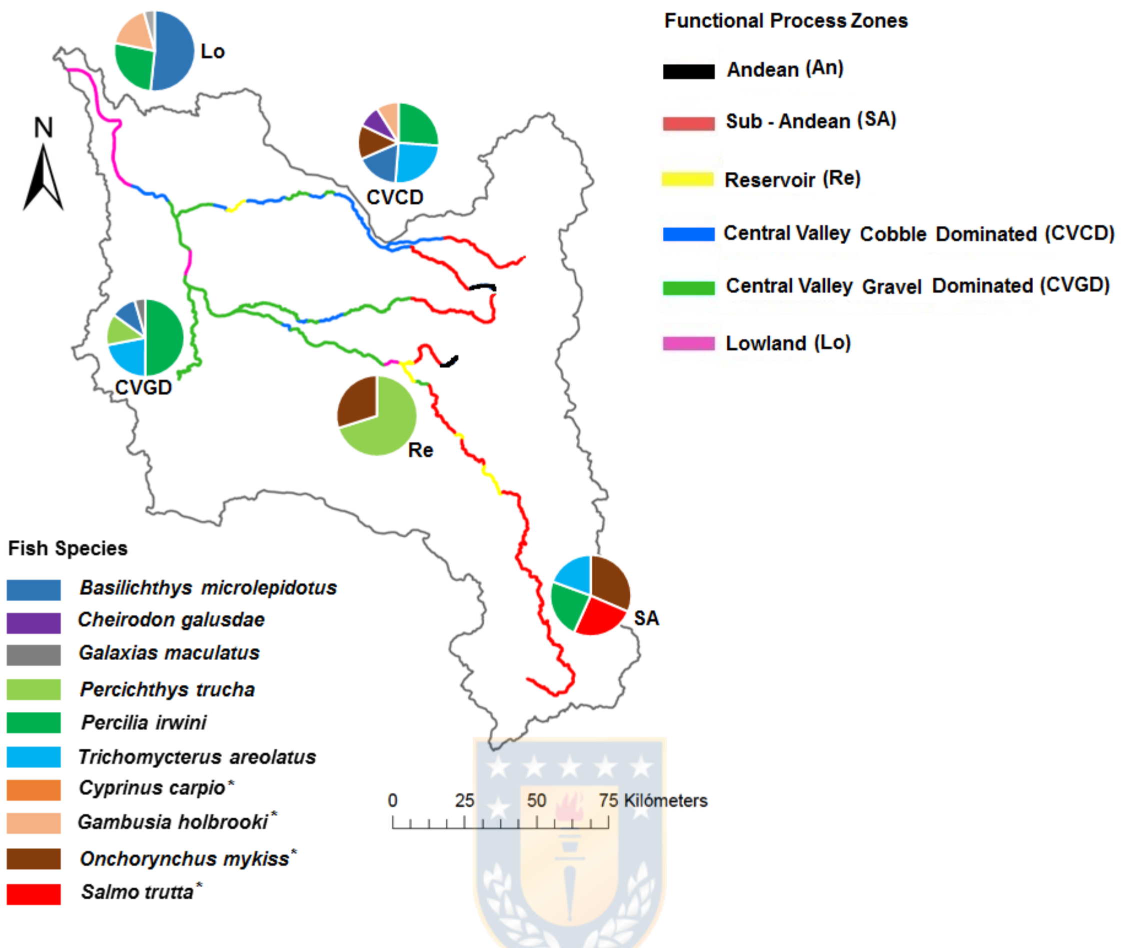

Figure 5.5. Fish community composition for each of the functional process zones in the Biobío River network. The pie chart represents the percentage of contribution of each species to the difference among FPZs (based on similarity percentage analysis

5.5 Discussion

This study of two Chilean Andean river networks demonstrates the application of a top-down hydrogeomorphic approach to assess the ecogeomorphological character research of river ecosystems. The network of the Biobío and Imperial Rivers are configured as a series of large-scale patches (FPZs); the spatial distribution of which do not resemble an orderly downstream progression of morphological adjustment or clinal pattern. The results indicate that downstream change in the hydrogeomorphic character of the Biobío and Imperial Rivers to be diverse and complex, instead of linear and predictable. Some FPZs repeated downstream, others were rare and only found in one river network, whereas others were relatively common. Of the seven FPZs that emerged through the analysis, two are found exclusively in the Biobío River and one in the Imperial River. Four abundant FPZs were common between the Biobío and Imperial river networks. These results contrast with the traditional view of rivers as a continuum (e.g., Leopold, Wolman, & Miller, 1964; Montgomery, 1999; Vannote et al., 1980), with predictable changes in physical and biological variables (riverbed sediments, water temperature, stream size, primary productivity, ecosystem respiration, invertebrate, and fish communities) from headwater regions to lowland areas. Thus, conventional approaches to managing the distribution of riverine habitats and associated biota that assume this predictable continuous change may be limited.

Physical habitat provides the template upon which evolution acts to create distinctive life history strategies (Southwood, 1977, 1988). Accordingly, the physical structure of river networks governs the type, abundance, and arrangement of biological communities found within these networks (cf. Thoms et al., 2018). This study has shown each FPZ in the Biobío River to have a unique fish community, similarly to specific macroinvertebrate communities and aquatic food web associated with FPZs character (Maasri et al., 2019; Thoms et al., 2017). Habitat use and adaptations of fish species, in this study, showed a clear relationship with the identified FPZs of the Biobío River. FPZ at high elevations (Sub-Andean) are dominated by the two most common nonnative salmonid species in Chile, rainbow trout and brown trout (*Salmo* *trutta*), typical of rivers with highly turbulent, well oxygenated waters, as well as coarse substrate (Habit, González, Ortiz-Sandoval, Elgueta, & Sobenes, 2015). FPZs with lower slopes and substrates of smaller size (i.e., the Central Valley Gravel Dominated FPZ) are preferentially inhabited by native species using both benthic and open water habitats. FPZs with a meandering river channel, low energies, and with wider floodplain, located in lowlands are dominated by both native and nonnative open water species, which prefer habitats of lower current velocity. Given these associations and the fact that various FPZs were common between the two analyzed river networks, we postulate that the same FPZs in the Imperial River network accommodate similar fish communities as their counterparts in the Biobío River network. Future studies of fish communities in these two river systems could be used to test this hypothesis and inform design of monitoring programmes. We recognize the limited number of sites where fish were collected, as they were sourced from existing monitoring databases. However, the results of this study align with previous research demonstrating associations between hydrogeomorphic and fish communities in river systems (cf. Boys & Thoms, 2006; Delong, Thoms, & Sorenson, 2019). Future studies incorporating more intense sampling of each of the FPZ are recommended to evaluate our hypothesis put forward in this study of Andean river systems.

FPZs and their link with particular fish communities can be instrumental in the design of monitoring programmes that account for the geomorphological and biological diversity of the entire river network. For instance, the specific character of the Sub-Andean FPZ combined with high abundances of nonnative trout causes lower abundances or absence of native fish (Habit et al., 2015). The prevalence of nonnative fish in Sub-Andean FPZ affect the integrity of fish native communities in this zone due to their impacts on native fish such as segregation, interspecific competition, and predation (Elgueta, González, Ruzzante, Walde, & Habit, 2013; Habit et al., 2010; Habit et al., 2015). Conversely, native fish appear to be favoured in FPZs at mid elevation and lower slopes and characterized by floodplain interactions as well as higher water temperatures and sediment loads less suitable for nonnative trout. These FPZs also provide spawning and juvenile rearing habitats for a range of these species (Górski, Habit, Pingram, & Manosalva, 2018; Montoya, Jara, Solis-Lufi, Colin, & Habit, 2012).

Differences in abundance and diversity of the FPZs and their link with particular fish communities can be instrumental in the design of monitoring programmes that account for the geomorphological and biological diversity of the entire river network. These FPZs form a refuge for native fish from trout invasion; however, their widespread through the network and high hydropower potential may make them susceptible to other anthropogenic disturbances such as fragmentation due to hydropower development (Díaz et al., 2019). Low abundance of a particular FPZ may indicate rare habitats and fish communities in the network. Tortuous alluvial FPZ in the Imperial River and Andean FPZ in the Biobío River could be examples of such singular FPZ. Fish community in these FPZ has not been characterized in monitoring programmes up to date. The abundance and character of different FPZs within the river network should be given special attention in development of monitoring programmes that aim at assessment of fish community in these rivers at the entire network scale.

This study demonstrates the physical character among FPZs to vary within Andean river networks and how this variability influences spatial variance of fish communities throughout the network. This implies that some FPZs may be more susceptible to anthropogenic stressors than others. Therefore, the conservation and management activities (assessment, restoration, and rehabilitation) can be more effective if they account for hydrogeomorphic variability within and across river networks. This effectiveness is essential and urgent for sustainable management and conservation of riverine fish communities in Andean river networks given the upcoming hydropower boom across Chilean rivers (Díaz et al., 2019).

The use of modern scientific concepts and methods in managing riverine landscapes is a measure of sound science and should always be employed when making decisions affecting the environment or natural resources (Cullen, 1990). To manage riverine ecosystems effectively and efficiently, the basic processes governing ecosystem structure and functioning must be understood at appropriate scales. This study of two Andean rivers provides a systematic approach to identifying FPZ and shows the close association between the physical character of FPZs and fish community composition. This in turn suggests that FPZs represent appropriate assessment targets for the conservation, rehabilitation, and management of entire riverine landscapes.

As demonstrated in two Chilean river systems, the spatial pattern of FPZs allows determination of abiotic and biotic attributes of a river network. Knowledge of the distribution of FPZs is especially useful where biotic data are limited or not available. Here, catchment-based conservation or management goals should focus on maintaining a representation of FPZs within a river network. Targets could be set to ensure that adequate lengths of each or certain FPZs within a network are conserved. Information on the distribution and character of FPZs should be combined with biotic information for each FPZ and conservation or management targets set. Moreover, FPZ with different anthropogenic stressors could be compared with those with no stress or alternative FPZs associated along stressor gradients could be determined within a catchment or a group of catchments to determine the possible presence of large-scale thresholds (Thorp et al., 2008). As such, we expect fish community parameters (abundance and diversity) to decrease in anthropogenically disturbed FPZs. Furthermore, the character of FPZ could mitigate the effects of disturbances, and this mitigation capacity is expected to vary among FPZs. This implies that some FPZs will be more susceptible to anthropogenic stressors than other.

5.6 Conclusion

This quantitative characterization of two Andean rivers has provided a detailed assessment of the composition and spatial organization of FPZs within these river networks. Furthermore, we documented that specific FPZs within a river network are inhabited by a particular fish community. This advances our understanding of the structural and ecological complexity of these rivers. The platform provided here may effectively assist river management applications and decision-making processes on a river network scale. Furthermore, it is an excellent tool for guiding designs of future ecological research and development of effective monitoring programmes.

5.7 Acknowledgements

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5.9 Appendix

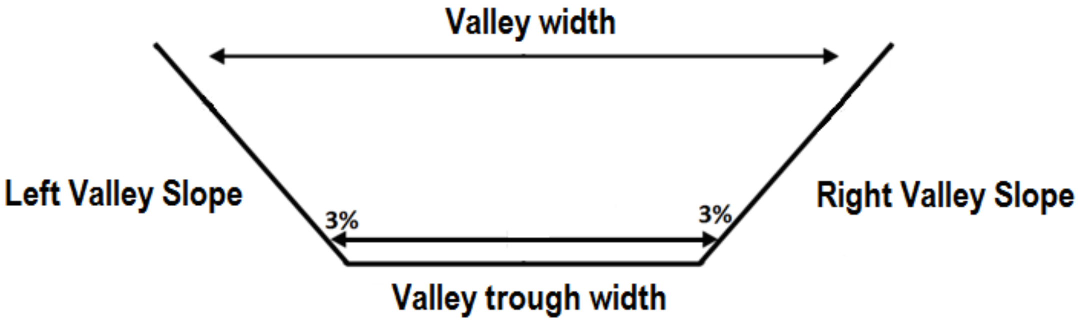

Figure 5.6. Squematic diagram of valley variables delineation.

Table 5.2. List of fish species found in Biobío River, some life history and habitat characteristics of these species and their distribution and abundance (Individual number) in Functional Process Zones (FPZs); Non-native species are indicated with asterisk (*).

Species name	**Common name**	**Life history**	**Habitat**	**Maximum body length (cm)**	**Feeding guild**	**SA**	**Re**	**CVGD**	**CVCD**	**Lo**
Basilichthys microlepidotus	Silverside	Resident	Open water	30	Omnivorous	3	15	139	505	150
Bullockia maldonadoi	Bagrecito	Resident	Benthic	8	Benthivorous	2		20	6	
Cheirodon galusdae	Pocha	Resident	Open water	7	Omnivorous	20		10	43	8
Diplomystes nahuelbutaensis	Tollo	Resident	Benthic	25	Benthivorous	23		10	10	
Galaxias maculatus	Puye	Resident Diadromous	Open water	12	Zooplanktivorous and Benthivorous	2		8		22
Odontesthes mauleanum	Cauque	Resident	Open water	30	Omnivorous			17		
Percichthys trucha	Perch	Resident	Open water	40	Benthivorous and Piscivorous	22	36	77	110	4
Percilia irwini	Darter	Resident	Open water	9	Benthivorous	213	1	329	182	35

Species name	**Common name**	**Life history**	**Habitat**	**Maximum body length (cm)**	**Feeding guild**	**SA**	**Re**	**CVGD**	**CVCD**	**Lo**
Trichomycterus areolatus	Catfish	Resident	Benthic	17	Benthivorous	93		93	95	1
*Australoheros facetus**	Chanchito	Resident	Open water	30	Omnivorous					3
*Carassius carassius**	Prussian carp	Resident	Open water	64	Omnivorous				1	
*Cyprinus carpio**	Common carp	Resident	Open water	120	Omnivorous			20	48	2
*Gambusia holbrooki**	Mosquitofish	Resident	Open water	10	Omnivorous			20	226	28
*Onchorynchus mykiss**	Rainbow trout	Resident	Open water	50	Benthivorous and Piscivorous	94	9	20	102	
*Salmo trutta**	Brown trout	Resident	Open water	50	Benthivorous and Piscivorous	156	1	1	11	
Number of Sampling Sites						**8**	**2**	**4**	**6**	**4**

Table 5.3. Contribution percentages (SIMPER) of species by functional process zones.

Functional process zones	Species	Average abundance	Average Similarity	Sim/SD	Percentage contribution	Cumulative contribution
Sub-Andean **Average similarity 49,04**	*Oncorhynchus mykiss*	3,97	15,23	1,49	31,06	31,06
	Salmo trutta	4,04	13,36	1,17	27,24	58,3
	Percilia irwini	4,14	10,11	0,72	20,61	78,9
	Trichomycterus areolatus	2,88	7,44	0,97	15,17	94,07
Central Valley Gravel Dominated **Average similarity: 50,39**	*Percilia irwini*	6,42	23,32	3,89	46,27	46,27
	Trichomycterus areolatus	3,24	10,15	1,78	20,15	66,41
	Percichthys trucha	2,59	6,06	0,9	12,03	78,44
	Basilichthys microlepidotus	3,21	4,91	0,53	9,75	88,19
	Galaxias maculatus	0,87	2,08	0,89	4,14	92,33
Central Valley Cobble Dominated **Average similarity: 39,96**	*Percilia irwini*	3,83	9,42	0,95	23,57	23,57
	Trichomycterus areolatus	2,56	9,02	1,36	22,57	46,13
	Basilichthys microlepidotus	3,44	6,18	0,6	15,45	61,58

Functional process zones	**Species**	**Average abundance**	**Average Similarity**	**Sim/SD**	**Percentage contribution**	**Cumulative contribution**
	Oncorhynchus mykiss	3,09	4,94	0,54	12,35	73,94
	Cheirodon galusdae	1,82	3,22	0,58	8,05	81,98
	Gambusia holbrooki	2,24	3,21	0,46	8,04	90,02
Lowland **Average similarity: 56,25**	*Basilichthys microlepidotus*	6,99	28,46	2,69	50,59	50,59
	Percilia irwini	3,76	12,94	13,9	23,01	73,6
	Gambusia holbrooki	2,94	8,65	2,26	15,38	88,98
	Galaxias maculatus	1,77	1,85	0,41	3,28	92,26
Reservoir **Average similarity: 54,51**	*Percichthys trucha*	7,42	38,22		70,11	70,11
	Oncorhynchus mykiss	3,61	16,3		29,89	100

6 CAPITULO II Alteraciones de caudal en la cuenca del río Biobío por la operación de centrales hidroeléctricas.

6.1 Introducción.

El abastecimiento de energía mediante hidroelectricidad ha adquirido un significativo rol en América Latina y Europa los últimos años (Solarin et al., 2015; Botelho et al., 2016). Hoy en día, existe una amplia variedad de tipos de proyectos hidroeléctricos, cada uno de los cuales, genera impactos ambientales y sociales de diferente naturaleza y magnitud (Egré & Milewski, 2002). Una de las particularidades de la hidroelectricidad, es que puede proporcionar energía base o continua durante todo el día o bien, ajustarse a los horarios con mayor demanda de energía. Esta particularidad, define una de las primarias consecuencias de la hidroelectricidad en los sistemas fluviales, la regulación y modificación de la variación natural del régimen de caudal (Opgrand et al., 2019). El avance de la construcción de centrales hidroeléctricas en todo el mundo ha provocado que casi dos tercios de los grandes ríos hayan sido modificados por represas (Nilsson et al., 2005; Fitzgerald et al., 2018). En Chile, aproximadamente 7.704 MW de energía es proporcionada por 142 centrales hidroeléctricas instaladas a lo largo del país (Ministerio de Energía, 2016). Se espera que este valor aumente progresivamente en el tiempo, dado el gran potencial hidroeléctrico del país (11 GW; Ministerio de Energía, 2016). El efecto de estas centrales en los sistemas fluviales de Chile ha sido pobremente estudiado por lo que, proponemos avanzar en el estudio de los efectos de centrales hidroeléctricas sobre los ríos de Chile, específicamente en las cuencas Andinas de Chile, la cuenca del río Biobío y la cuenca del río Imperial.

La cuenca del río Biobío, en la actualidad cuenta con 11 grandes centrales hidroeléctricas instaladas y en operación, distribuidas en los ríos Biobío, Duqueco, Laja y Rucúe. De acuerdo con la capacidad de almacenamiento de agua, estas centrales se pueden clasificar en centrales con embalse (5 centrales hidroeléctricas) o de pasada (6 centrales hidroeléctricas; Tabla 6.2

Tabla 6.1). Además, en la actualidad dos centrales hidroeléctricas se encuentran aprobadas en el Servicio de Evaluación Ambiental, pero sin iniciar su construcción aún (Centrales hidroeléctricas Rucalhue y Frontera). La primera central hidroeléctrica operativa en el curso principal del río Biobío data del año 1996, con la instalación y operación de la central hidroeléctrica de embalse Pangue. Desde entonces se le han sumado 2 plantas hidroeléctricas de tipo embalse, Central hidroeléctrica Ralco (2004) y Central hidroeléctrica Angostura (2014). En el río Laja, afluente septentrional del río Biobío, la instalación y operación de la primera central hidroeléctrica data del año 1948-1952, con la puesta en marcha de la Central hidroeléctrica Abanico y posteriormente se le adiciona las centrales hidroeléctricas El Toro (1973) y Antuco (1981). Los efectos de estas centrales en la cuenca del río Biobío han sido previamente estudiados, en términos de su impacto sobre la comunidad de peces y sobre los hábitats de estos (Habit et al., 2007; García et al., 2011). Tales estudios dejaron en evidencia cambios en los ensambles de peces en la cuenca del río Laja (Habit et al., 2007), así como también, modificaciones de los hábitats idóneos para peces en términos de cantidad, calidad y ubicación de los diferentes hábitats en el río Biobío (García et al., 2011). De manera más reciente, Díaz et al. (2019), describen a la cuenca del río Biobío como una cuenca altamente fragmentada por centrales hidroeléctricas, lo que, sin duda, modifica la conectividad del río para el desarrollo de los procesos propios del ecosistema. Cabe destacar que ninguno de estos estudios ha abarcado directamente el efecto de la operación de las centrales hidroeléctricas sobre caudal de la cuenca del río Biobío. Por lo que el objetivo central de este capítulo es estudiar este efecto, analizando el caudal del río Biobío, a escala horaria, diaria y largo plazo en zonas de procesos funcionales con y sin regulación. Para abordar este objetivo, y en la pausible posibilidad de no encontrar FPZs sin regulación hidrológica, propusimos la búsqueda de zonas de procesos funcionales de referencia sin alteración hidrológica en la cuenca del río Imperial. La elección de esta cuenca como una cuenca de referencia se basó en una evaluación de las características ambientales y ecológicas, tales como, zonas de procesos funcionales similares, clima, precipitación, régimen de caudal, calidad de aguas y alta similitud en composición de macroinvertebrados y peces (Ver Introducción y Capítulo I).

6.2 Metodología

6.2.1 Área de estudio

Este estudio fue realizado en las cuencas de los ríos Biobío e Imperial. Dada la dificultad para encontrar sitios con caudal no perturbado en la cuenca del río Biobío, la cuenca del río Imperial fue caracterizada en términos de sus caudales como una cuenca de referencia, o caudal natural. La cuenca del río Biobío posee un área de 24,029 km^2, localizada entre los 36° y 39° de latitud sur. Este río nace en la Cordillera de los Andes (1500 msnm), fluye en dirección este-oeste durante 407 km antes de desembocar en el océano Pacífico. Su caudal medio anual es de aproximadamente 900 m^{3}s^{-1} en sus tramos bajos (Niemeyer y Cereceda, 1984). La cuenca del río Imperial se extiende entre los 37° y 38° latitud sur, y posee un área de 12,054 km^2. Esta cuenca nace en la Cordillera de los Andes (1400 msnm), tiene una longitud total de 230 km y su caudal medio anual es de aproximadamente 240 m^{3}s^{-1} en sus tramos bajos (Niemeyer & Cereceda, 1984). El clima de ambas cuencas es húmedo-templado con influencia mediterránea. Su precipitación anual varía entre 1200 a 4000 mm. Como resultado, los caudales en ambas cuencas son generalmente más altos entre los meses de julio y noviembre (invierno y primavera). Se considera que ambas redes fluviales son altamente vulnerables al cambio climático debido a los aumentos de temperatura proyectados y la disminución de las precipitaciones en las próximas décadas (Panel Intergubernamental para el Cambio Climático, 2015). En lo que respecta a su geomorfología, ambas cuencas hidrográficas comparten 4 zonas de procesos funcionales (Sub-Andean, Central Valley Cobble Dominated, Central Valley Gravel Dominated y Lowland, ver Capítulo I). Además, cada una de estas cuencas presentan zonas de procesos funcionales (FPZs) singulares y únicas en su extensión, correspondiente a Andean y Reservoir FPZs en la cuenca del río Biobío y Tortuous Alluvial en la cuenca del río Imperial.

Tabla 6.1. Principales características de las 11 centrales hidroeléctricas en la cuenca del río Biobío y la ubicación espacial de la infraestructura hidroeléctrica en las zonas de procesos funcionales (FPZ; ver Capítulo I).

Central hidroeléctrica	Ubicación	Tipo según capacidad de almacenamiento	Potencia instalada MW	Año que entró en operación	FPZ
Ralco	Río Biobío	Embalse	467	2004	Sub-Andean
Pangue	Río Biobío	Embalse	690	1996	Sub-Andean
Angostura	Río Biobío	Embalse	316	2014	Central Valley Gravel Dominated
Mampil	Río Duqueco	Pasada	55	2000	Sub-Andean
Peuchén	Río Duqueco	Pasada	85	2000	Sub-Andean
Antuco	Río Laja	Pasada	300	1981	Sub-Andean
Abanico	Río Laja	Pasada	93	1952	Sub-Andean
Quilleco	Río Laja	Pasada	71	2007	Central Valley Cobble Dominated
Rucúe	Río Rucúe	Pasada	178	1998	Central Valley Cobble Dominated
Laja	Río Laja	Embalse	34	2013	Central Valley Cobble Dominated
Toro	Río Laja	Embalse	450	1973	Sub-Andean

6.2.2 Generación eléctrica

A partir de los datos proporcionados (Mega Watts hora, MWh) por el Coordinador eléctrico Nacional (CEDEC-SIC) se realizó un análisis del promedio y desviación estándar de los MWh generados por cada central hidroeléctrica. Para ello, se utilizaron los datos de generación eléctrica a escala horaria durante un año (2013). Esto permitió determinar el tipo de generación eléctrica que posee cada central hidroeléctrica: generación continua o base (run-of-river) o con picos de generación asociada a la demanda eléctrica (Hydropeaking; Egré & Milewski 2002; Kuriqi et al., 2018). A partir de este análisis, se determinaron tres tipos de categorías de caudal: caudal natural (en adelante, “natural flow”), generación continua (en adelante, “run-of-river”) y generación de punta (en adelante, “hydropeaking”).

6.2.3 Variables hidrológicas.

Los datos de caudal diario y sub-diario fueron recopilados a partir de 15 estaciones hidrométricas (N=30 años aproximadamente, 1986 al 2016), 11 ubicadas en la cuenca del río Biobío y 4 en la cuenca del río Imperial. Estas estaciones hidrométricas pertenecen a la Dirección General de Aguas (DGA). A partir de estos datos de caudal se calcularon 41 índices hidrológicos para cada estación hidrométrica (Tabla 6.2), que representan los 5 componentes del régimen de caudal, vale decir, magnitud, frecuencia, duración, *timing* y tasa de cambio (cf. Richter et al., 1997 & 1998; Thoms and Parsons, 2003). Estos índices hidrológicos permiten la caracterización de los caudales en tres escalas de tiempo; sub-diario, diario y largo plazo (anual). Para determinar la diferenciación de caudales entre los tres tipos de categorías de caudal - natural flow, run-of-river y hydropeaking- se empleó un análisis permutacional de varianza (PERMANOVA; Anderson, 2017). Debido a que no existen diferencias significativas entre los índices de natural flow registrados entre los ríos Biobío e Imperial (Permanova, Pseudo-F: 0,6446; P perm: 0,60), para efecto del análisis de PERMANOVA para la categoría natural flow se consideran los valores registrados para ambos ríos.

Figura 6.1. Estaciones hidrométricas en las cuencas de los ríos Biobío e Imperial.

Tabla 6.2. Índices hidrológicos estimados para analizar el régimen de caudal en las cuencas de los ríos Biobío e Imperial. Escala de análisis de datos sub-diario (SD), diario (D) y largo plazo (LT)

Índice hidrológico	**Escala de tiempo**	**Descripción**
Fluctuaciones de caudal sub-diarias	SD	Diferencia entre el máximo y el mínimo caudal diario. Este valor es normalizado por el caudal promedio diario, con el objetivo de considerar las diferencias a escala de ríos y cuencas.
Tasa de incremento de caudal	SD	Cambios en el caudal entre dos sucesivas observaciones de caudal, dividido por el tiempo de observación del intervalo.

Índice hidrológico	Escala de tiempo	Descripción
Coeficiente de variación de la tasa de incremento de caudal.	SD	Tasa de incremento dividido por la mediana del caudal diario.
Tasa promedio de incremento de caudal	SD	Tasa promedio de cambios positivos en el caudal desde un día al siguiente día dividido por el caudal promedio diario.
Tasa promedio de descenso de caudal	SD	Tasa promedio de cambios negativos en el caudal desde un día al siguiente día dividido por el caudal promedio diario
Coeficiente de variación en términos de descenso e incremento de caudal	SD	Tasa de descensos e incrementos dividida por caudal medio diario.
Caudal mínimo diario	SD	Caudal mínimo medido en 24 hrs (Qmin).
Caudal máximo diario	SD	Caudal máximo medido en 24 horas (Qmax).
Caudal delta diario	SD	Diferencia entre caudal mínimo y caudal máximo. Representa la cantidad de cambios diarios de caudal.
Desviación estándar	SD	Desviación estándar estadística de caudal en un tiempo de 24 horas.
Reversión (descenso e incrementos)	SD	Números de cambios entre incrementos y descensos de caudal.
Variabilidad de caudales diarios	D	Caudal promedio diario por un año y luego promediado entre años.
Caudal promedio diario	D	Caudal medio diario
Mediana de caudal diario	D	Mediana de caudal diario
Asimetría de caudales diario	D	Caudal medio diario dividido por la mediana del caudal diario.

Índice hidrológico	Escala de tiempo	Descripción
Rangos de caudales diarios (10/90th), (25/75th)	D	Proporción de caudales diarios encontrados dentro de los percentiles diarios 10th/90th y 25th/75th
Spreads de caudales diarios (10/90th), (25/75th)	D	Rangos de caudales diarios divididos por el promedio de caudal diario.
Caudal mínimo y máximo anual de 1-/3-/7-/30-/90-dias	LT	Magnitud del mínimo o máximo caudal anual en 1-/3-/7-/30 /90-dias.
Variabilidad anual en caudal mínimo y máximo de 1-/3-/7-/30 /90-dias	LT	Coeficiente de variación de la magnitud del mínimo o máximo caudal anual en 1-/3-/7-/30 /90-dias dividida por el caudal medio diario.

6.2.4 Análisis espaciales y estadísticos.

Se avaluó espacialmente la distribución de las centrales hidroeléctricas en la cuenca del río Biobío y en específico en las zonas de procesos funcionales, utilizando como herramienta el programa ArcGis 10.5. Con el fin de obtener aquellos índices que explican una mayor cantidad de varianza entre las categorías de caudal se utilizó el análisis de componentes principales (PCA).

6.3 Resultados

6.3.1 Generación eléctrica.

En la cuenca del río Biobío se observan dos tipos de generación eléctrica, una en base a picos de generación eléctrica (hydropeaking) con alta variabilidad diaria, contrastada con una generación base con producción de electricidad de manera constante y con baja variabilidad diaria (run-of-river; Figura 6.2). La generación eléctrica de tipo hydropeaking se observó en dos ríos específicos de la cuenca del río Biobío, en el río Duqueco y el río Biobío. La variabilidad diaria, en cuanto a la generación eléctrica medida como MWh, es mayor en el río Biobío que en el río

Duqueco. La generación de tipo run-of-river es generada en su totalidad en el río Laja y la variabilidad en cuanto a MWh producido es baja.

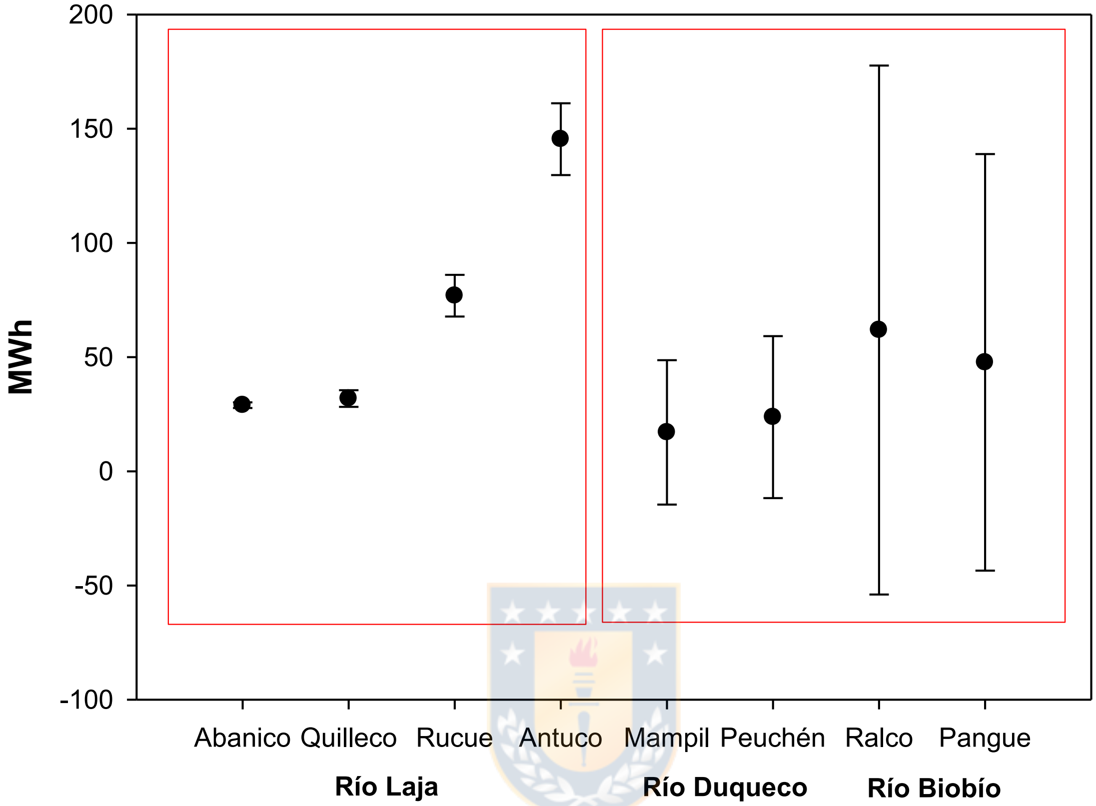

Figura 6.2. Generación eléctrica promedio y desviación estándar, analizada a escala horaria por un año en 8 centrales hidroeléctricas de la cuenca del río Biobío.

6.3.2 Diferenciación hidrológica del caudal natural, hydropeaking y run-of-river.

Basado en los índices hidrológicos, se detectaron diferencias significativas entre las tres categorías de caudal presentes en el río Biobío (PERMANOVA, Pseudo-F: 4,2447; P perm: 0,0009). Del total de kilómetros de red hídrica analizada en el río Biobío (800 km, equivalentes a 11,7% del total de ríos la cuenca), sólo el 29% de los tramos de río analizado (230 Km, 3,4% del total de ríos de la cuenca) mantienen un régimen de caudal natural. Estos tramos con caudal natural se caracterizan por bajas fluctuaciones sub-diarias (fluctuaciones de caudal sub-diarias: 0,10) y una tasa de cambio de caudal sub-diario de 0,09 m^3/s^{-1} h^{-1}. Además, los cambios en su caudal no superan los 11 m^3/s en 24 horas (Tabla 6.3, Figura 6.4).

De los 800 Km estudiados, 275 Km de río presentan un flujo alterado por la operación hydropeaking (34% de lo analizado y 4,0% del total de ríos de la cuenca). Este caudal se caracteriza por alta variabilidad (fluctuaciones de caudal sub-diarias: 0,82) y fuerte tasa de cambio diaria de 35,37 m^3/s^{-1} h^{-1} a escala sub-diaria (Tabla 6.3 y Figura 6.4). En 24 horas, este tipo de operación puede producir cambios en una magnitud de 156 m^3/s de caudal. Los hidrogramas anuales de las secciones del río con hydropeaking muestran un patrón de estacionalidad similar a caudal natural (Figura 6.5). No obstante, diferencias significativas fueron observadas entre los caudales diarios y sub-diarios obtenidos en natural flow y hydropeaking (PERMANOVA: Pseudo F: 9,73; p: 0,003). Las variables sub-diarias y diarias que representan la variabilidad de caudal a esas escalas temporales, en términos de magnitud, frecuencia y tasas de cambio explican con mayor fuerza la variabilidad de los tramos con y sin regulación de caudal (Figura 6.6). Además, en la Figura 6.6 se observa en el PC2 una diferenciación entre ríos con alteración de tipo hydropeaking, en donde el hydropeaking del río Biobío es caracterizado por cambios bruscos en la magnitud de caudal y alta variación subdiaria, mientras que el río Duqueco es caracterizado por un alto numero de aumentos y descensos de caudal a escala subdiaria.

Tabla 6.3. Promedio y desviación estándar de índices hidrológicos por categoría de caudal en el río Biobío: natural flow (NF), run-of-river (ROR) y hydropeaking (HP).

Parámetros hidrológicos	**Escala temporal**	**NF**		**ROR**		**HP**	
		Promedio	**Desviación estándar**	**Promedio**	**Desviación estándar**	**Promedio**	**Desviación estándar**
Fluctuaciones de caudal sub-diarias	Sub-diario	0,10	0,02	0,38	0,24	0,82	0,34
Tasa promedio de incremento mínimo de caudal		0,00	0,00	0,05	0,06	0,63	0,84
Tasa promedio de incremento máximo de caudal		3,15	1,64	24,66	43,91	102,60	72,92
Tasa promedio de incremento de caudal		0,09	0,14	9,24	19,17	35,37	29,23
Tasa de incremento de caudal		9,00	10,30	12,50	10,47	35,36	35,57
Tasa de descenso de caudal		4,34	3,53	14,89	10,46	31,82	29,58
Coeficiente de variación en términos de descensos de caudal diario		1,70	0,45	2,39	0,69	1,58	0,41
Coeficiente de variación en términos de incrementos de caudal		1,79	0,57	2,67	0,90	1,66	0,39
Caudal mínimo diario		68,26	33,52	74,74	45,41	156,60	123,85
Caudal máximo diario		79,97	36,79	123,27	110,51	312,71	211,31
Caudal delta diario		11,71	3,75	23,30	13,16	155,77	103,05
Desviación estándar del caudal diario		3,81	1,20	21,27	22,02	50,62	34,28
Descensos de caudal diario (Reversión)		148,30	117,18	2449,88	4657,31	5118,67	4945,49
Incrementos de caudal diario (Reversión)		220,20	185,17	2614,75	5508,83	5800,67	5685,03

Parámetros hidrológicos	**Escala temporal**	**NF**		**ROR**		**HP**	
		Promedio	**Desviación estándar**	**Promedio**	**Desviación estándar**	**Promedio**	**Desviación estándar**
Caudal promedio diario	Diario	74,48	35,82	98,93	75,09	231,41	163,35
Mediana de caudal diario		64,27	39,58	99,48	78,82	226,16	172,32
Asimetría de caudal diario		1,50	0,77	1,20	0,44	1,26	0,41
Variabilidad en caudales diario		0,06	0,03	0,16	0,07	0,24	0,06
Rangos de caudales diario (10/90th),		0,91	0,04	0,79	0,13	0,70	0,17
Rangos de caudal diario (25/75th)		0,94	0,02	0,86	0,09	0,72	0,10
Spreads de caudales diarios (10/90th),		0,04	0,06	0,03	0,04	0,02	0,03
Spreads de caudales diarios (25/75th)		0,04	0,06	0,03	0,04	0,01	0,02
Caudal máximo anual de 1 día	Largo plazo	366,68	189,97	532,62	220,52	1044,98	812,47
Caudal máximo anual de 3 días		324,53	169,38	446,41	203,59	930,43	760,73
Caudal máximo anual de 7 días		277,18	146,59	371,87	180,03	802,28	679,99
Caudal máximo anual de 30 días		193,35	103,10	242,86	148,52	574,10	465,66
Caudal máximo anual de 90 días		154,96	83,90	199,20	126,65	447,09	351,58
Caudal mínimo anual de 1 día		17,85	12,28	15,99	15,34	49,30	43,91
Caudal mínimo anual de 3 días		17,97	12,33	17,52	17,50	51,91	45,43
Caudal mínimo anual de 7 días		18,24	12,43	18,92	19,15	56,18	48,15

Parámetros hidrológicos	Escala temporal	NF		ROR		HP	
		Promedio	**Desviación estándar**	**Promedio**	**Desviación estándar**	**Promedio**	**Desviación estándar**
Caudal mínimo anual de 30 días		19,55	13,05	23,07	21,38	66,89	54,70
Caudal mínimo anual de 90 días		22,42	14,22	31,95	27,47	81,14	61,69
Variabilidad anual en caudal máximo 1 día		0,58	0,14	0,61	0,07	0,96	0,53
Variabilidad anual en caudal máximo 3 días		0,55	0,13	0,59	0,06	0,59	0,20
Variabilidad anual en caudal máximo 7 días		0,55	0,15	0,61	0,09	0,55	0,16
Variabilidad anual en caudal máximo 30 días		0,61	0,23	0,71	0,20	0,54	0,15
Variabilidad anual en caudal máximo 90 días		0,60	0,41	0,75	0,32	0,55	0,19
Variabilidad anual en caudal mínimo 1 día		0,23	0,17	0,79	0,56	0,26	0,05
Variabilidad anual en caudal mínimo 3 días		0,25	0,25	0,73	0,50	3,38	7,65
Variabilidad anual en caudal mínimo 7 días		0,71	1,71	0,71	0,48	0,28	0,07
Variabilidad anual en caudal mínimo 30 días		0,39	0,64	0,69	0,38	0,34	0,15
Variabilidad anual en caudal mínimo 90 días		0,35	0,22	0,55	0,14	0,39	0,13

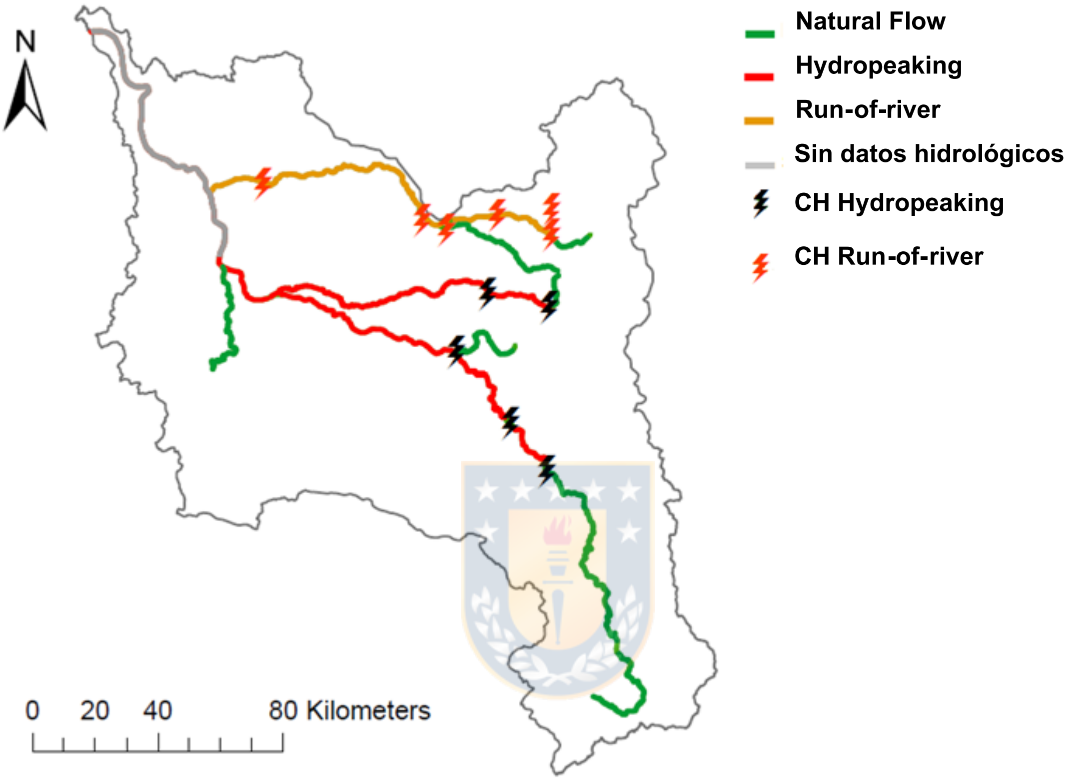

Figura 6.3. Distribución espacial de tramos de río con natural flow, hydropeaking y run of river en la cuenca del río Biobío.

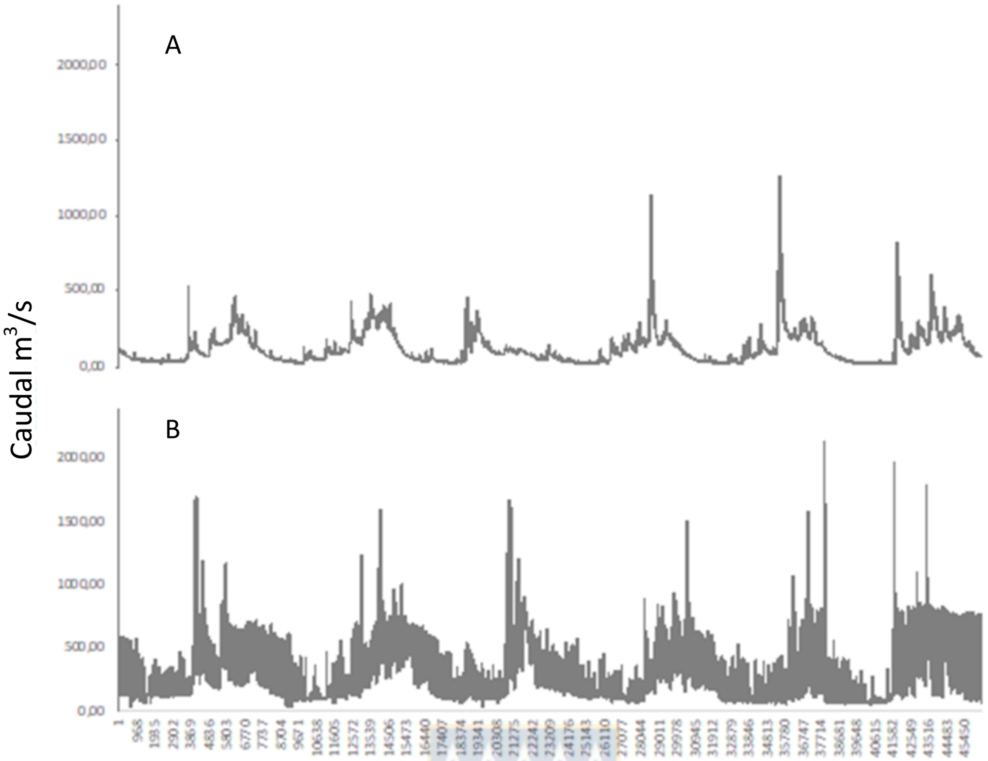

Figura 6.4. Hidrograma del río Biobío en tramos con A) Caudal Natural, B) Caudal alterado por hydropeaking. Datos de caudal sub-diario 2010 a 2015.

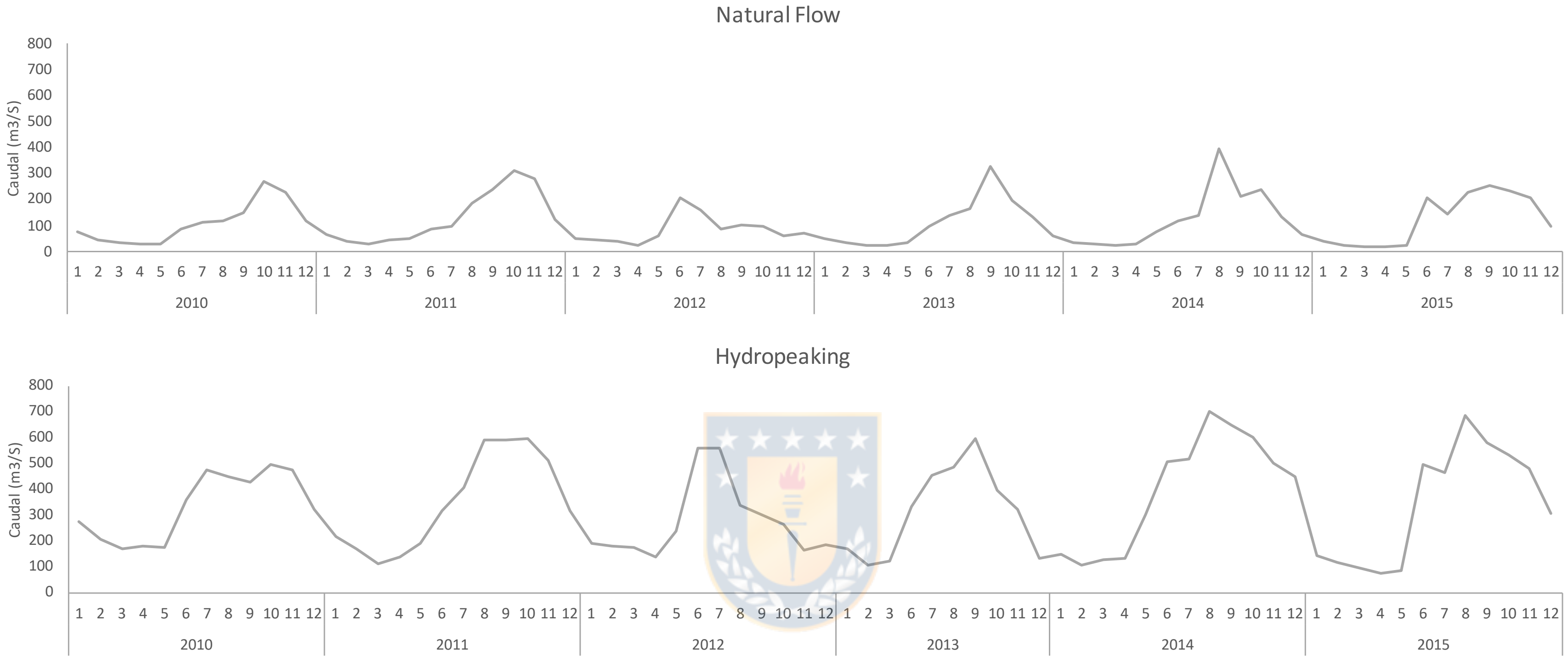

Figura 6.5. Caudal medio mensual (m^3/s) de secciones de río Biobío con caudal natural y secciones alteradas por centrales hidroeléctricas con operación hydropeaking.

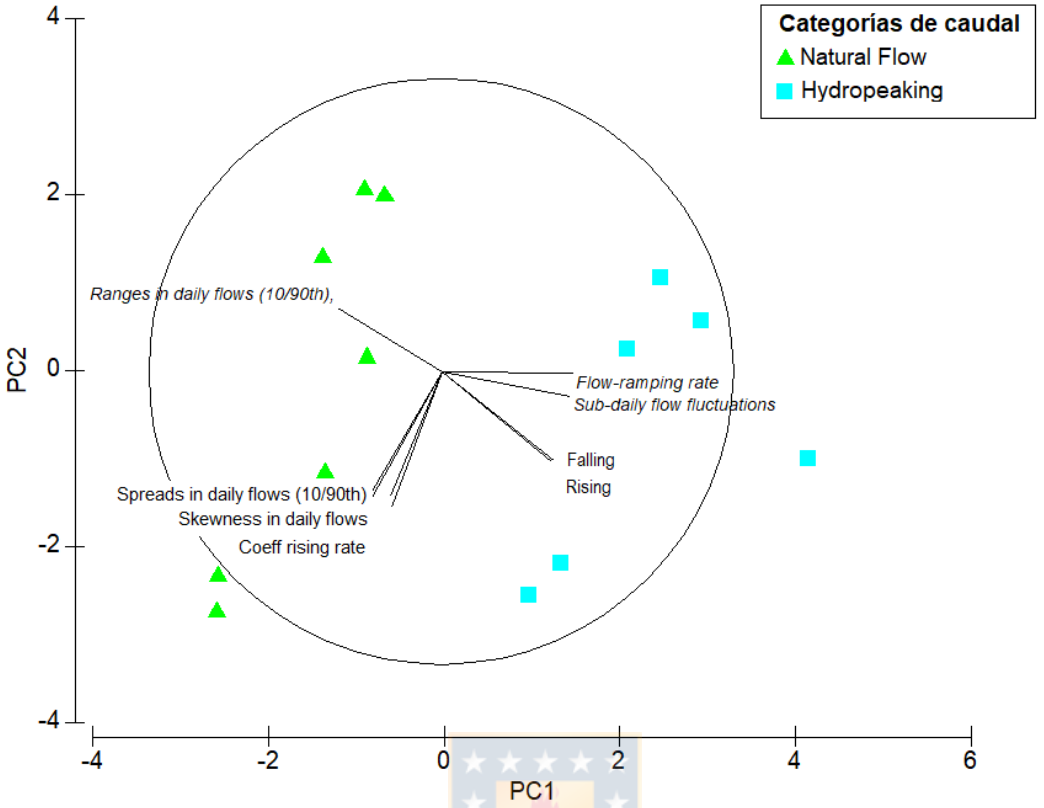

Figura 6.6. Análisis de componentes principales (PCA) de categorías de caudal (natural flow y hydropeaking) basado en los indicadores hidrológicos. Los dos primeros ejes explican el 86% de la varianza. Las variables se muestran en la Tabla 6.2.

Por último, 220 km de río se encuentran alterados por operación run-of-river (27,5% de los ríos estudiados y 3,2% del total de ríos la cuenca). Este tipo de operación registra un incremento de las fluctuaciones de caudal sub-diario (fluctuaciones de caudal sub-diarias: 0,38) y una tasa de cambio de 9,24 m^3/s^{-1} h^{-1}. Así mismo, se registra que 23,3 m^3/s es la magnitud del caudal que cambia en 24 horas. En cuanto a la comparación entre caudal natural y run-of-river se registraron diferencias significativas en los parámetros analizados (Permanova: Pseudo F: 8,13; p: 0,0001), con un aumento de la magnitud promedio desde 74,48 a 98,93 m3/s, como también la tasa de cambio y la frecuencia de las fluctuaciones del caudal en run-of-river (Figura 6.7 y Figura 6.8). En cuanto a su estacionalidad, no se observan cambios en los valores máximos de caudal de manera anual. En la Figura 6.9 se observa una diferenciación entre aquellos puntos con categorías de caudal run-of-river ubicados en el río Rucúe y Laja. En específico, en el río Laja la categoría de caudal run-of-river se caracteriza por cambios en la tasa de variación sub-diario de caudal, mientras que en el río Rucúe se observa que esta categoría es caracterizada por variación a escala temporal diaria.

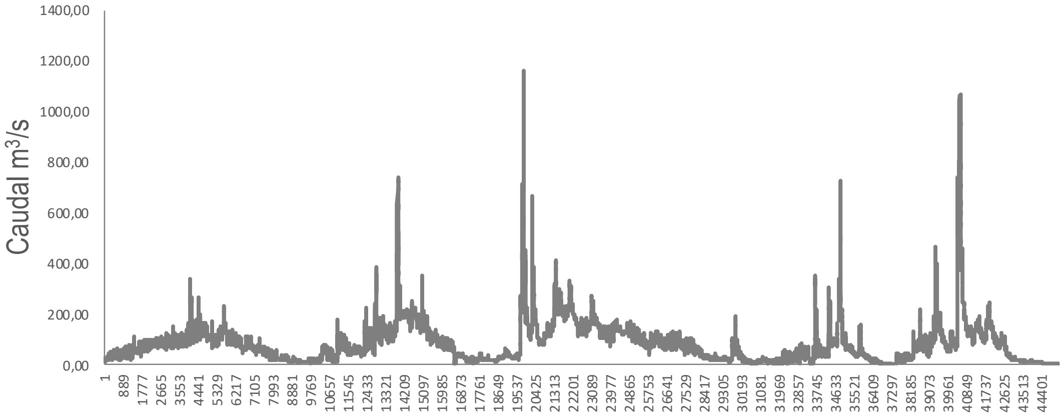

Figura 6.7. Hidrograma del río Laja en tramos con caudal regulado por centrales de run-of-river. Datos de caudal sub-diario 2010 a 2015.

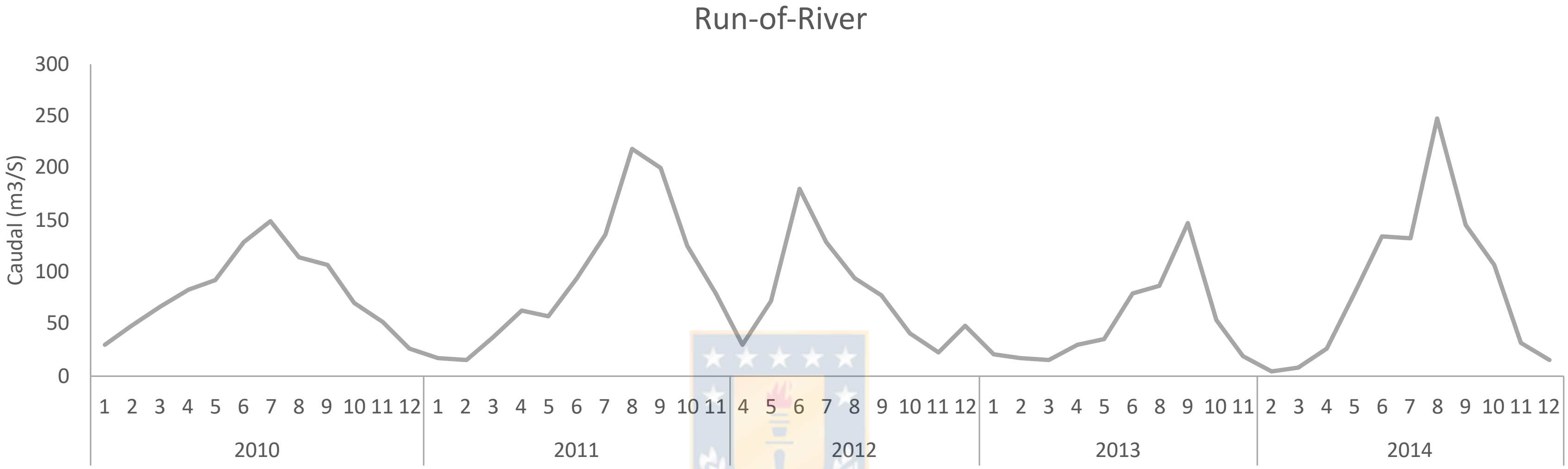

Figura 6.8. Caudal medio mensual (m^3/s) de secciones de río con caudal alterado por centrales hidroeléctricas con operación run-of-river.

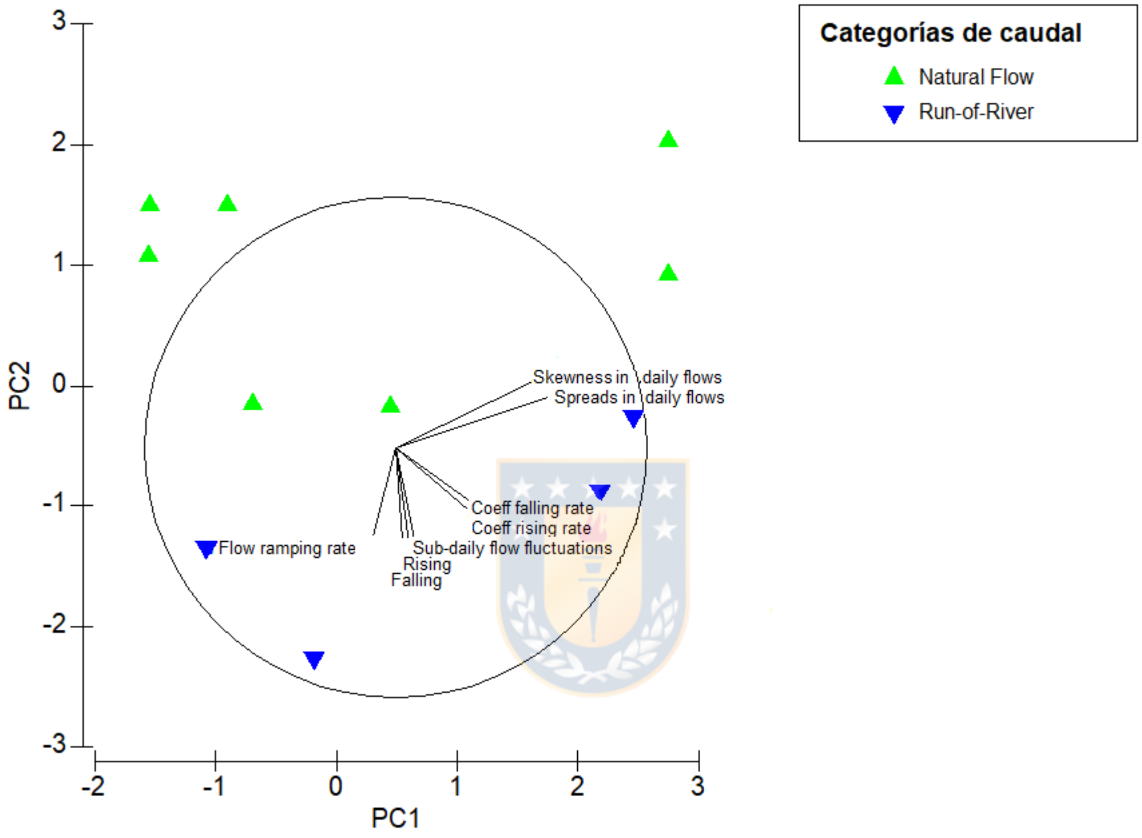

Figura 6.9. Análisis de componentes principales (PCA) de categorías de caudal (natural flow y run-of-river) sobre los indicadores hidrológicas. Los dos primeros ejes explicaron el 82% de la varianza.

6.3.3 Distribución espacial de las centrales hidroeléctricas en las FPZs

El análisis de la distribución espacial de las centrales hidroeléctricas, a lo largo de la red hídrica de la cuenca del río Biobío, detalla que las centrales hidroeléctricas con operación de tipo hydropeaking, se encuentran localizadas principalmente en la zona de proceso funcional Sub-Andean. No obstante, y debido a las fuertes fluctuaciones que establecen en el caudal, impactan fuertemente la zona de proceso funcional denominada Central Valley Gravel Dominated. Las centrales hidroeléctricas con operación de tipo run-of-river se encuentran localizadas en la zona Sub-Andean y Central Valley Cobble Dominated del río Laja. No obstante, la zona mayormente afectada por este tipo de operación es la denominada Central Valley Cobble Dominated. Cabe destacar, que esta zona de proceso funcional (CVGD) se encuentra alterada en toda su extensión dentro de la cuenca del río Biobío. En cuanto a tramos del río con caudal natural, se observa que, dentro del área de estudio mantienen esta condición, parches de la zona de proceso funcional Sub-Andean y Central Valley Gravel Dominated (Río Vergara principalmente). Por último, en el río Imperial, existe solo una central hidroeléctrica ubicada en un pequeño tributario de la cuenca del río Imperial (río Trueno) en la zona de proceso funcional Central Valley Cobble Dominated.

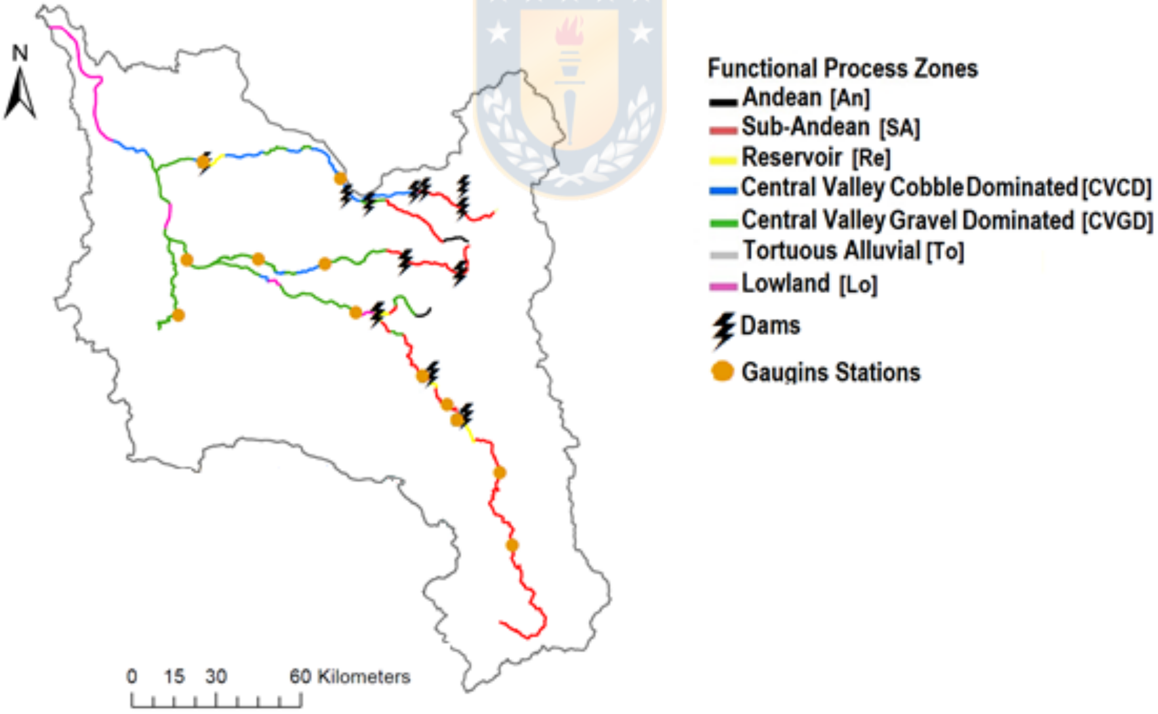

Figura 6.10. Distribución espacial de centrales hidroeléctricas (dams) en relación con las zonas de procesos funcionales (FPZs: SA = 7 centrales hidroeléctricas;

CVCD = 3 centrales hidroeléctricas; CVGD: 1 central hidroelectrica). Se indica también la posición de la estaciones fliviométrica DGA (gaugins stations).

6.4 Discusión

El caudal de la cuenca del río Biobío se encuentra fuertemente regulado por centrales hidroeléctricas. Actualmente se distinguen tres categorías de régimen de caudal en esta cuenca, correspondientes al régimen natural (natural flow), régimen alterado por centrales de pasada (run-of-river) y régimen alterado por central con operación de punta (hydropeaking). El régimen de hydropeaking se produce en los ríos Biobío y Duqueco, debido a la presencia de las entrales Ralco, Pangue y Pangue, y Mampil y Peuchén, respectivamente. Este tipo de alteración genera significativas alteraciones respecto del caudal natural a escala temporal sub-diaria y diaria. Sin embargo, de acuerdo con nuestros resultados, no genera cambios estadísticamente significativos en los patrones estacionales anuales del caudal. La alteración de caudal generada por la operación de tipo run-of river, se ubica exclusivamente en la cuenca del río Laja. Al igual que la alteración por hydropeaking, este tipo de operación genera un aumento en la variabilidad de los caudales diarios y sub-diarios en los tramos analizados, pero en una magnitud menor.

De los 800 Km de río estudiados, 495 Km presentan algún tipo de regulación de caudal y abarcan las tres principales zonas de procesos funcionales encontradas en el río Biobío (61,9% de los tramos estudiados y 7,1% del total de ríos de la cuenca). Las zonas de procesos funcionales Sub-Andean y Central Valley Gravel Dominated presentan mayoritariamente alteración de tipo hydropeaking. Mientras que la zona de proceso funcional Central Valley Cobble Dominated presenta alteración de tipo run-of-river.

Se demostraron severas alteraciones del caudal natural del río Biobío a causa de la operación de tipo hydropeaking. Similares efectos han sido reportados en otros sistemas fluviales, tales como en Norte América, China y Europa (Bejarano et al., 2017; Hecht et al., 2019). El hydropeaking se ha descrito como un tipo de operación que afecta gravemente las variables hidrológicas que describen el régimen de caudal a escalas temporales, diarias y sub-diarias (Bruno et al., 2010; Ashraf et al., 2018). En conformidad a ello, nuestros resultados describen un cambio dramático en la variabilidad del flujo diario y sub-diario en los tramos evaluados en el río Biobío y Duqueco, descrito a través de índices, tales como, el coeficiente de variación, conteo de incrementos y los descensos de caudal a nivel diario y sub-diario (Bejarano et al., 2017).

En las últimas décadas las centrales hidroeléctricas del tipo run-of-river, han surgido como una alternativa a la construcción de centrales hidroeléctricas con embalses, debido a su menor costo económico y social (Postel et al. 1996; Abbasi & Abbasi 2011; Anderson, 2014). Estas centrales hidroeléctricas han sido catalogadas como una alternativa, con menores efectos a nivel ecológico. No obstante, hoy en día, esta perspectiva es desafiada por diferentes estudios, en los que también se reconocen efectos no deseados de estas centrales sobre los procesos ecológicos de los ríos (Anderson, 2014). Es más, se ha descrito que múltiples centrales de tipo run-of-river en una misma cuenca podrían tener impactos aún mayores que una central hidroeléctrica con embalse, como consecuencia de acumulativos impactos en la cuenca, en donde frecuentes y grandes tramos de ríos se encuentran sometidos a caudal mínimo ecológico, pérdida de hábitats de rápidos, reducción general de hábitats, acumulación de sedimentos y materia orgánica (Santucci et al. 2005; Bakken et al. 2012; Kibler & Tullos, 2013). Todos estos impactos de las plantas hidroeléctricas a escala pequeña amenazan poblaciones de macroinvertebrados y peces (Larinier, 2008). En cuanto a los efectos de la operación run-of-river sobre el caudal, nuestros resultados describen que, en aquellos tramos aguas abajo de la turbina, se generan fluctuaciones de caudal como resultado de aumentos o disminuciones intencionales en la proporción del caudal desviado a las turbinas, para optimizar la producción de electricidad. Estos resultados concuerdan con los obtenidos por Almodüvar & Nicola (1999) y Gibeau et al. (2016).

En los ríos intervenidos por hidroelectricidad, el grado de alteración de los caudales es establecido por las reglas de operación de cada central hidroeléctrica (Opgrand et al., 2019). La magnitud de los cambios causados por el hydropeaking y/o run-of-river sobre los procesos fluviales dependen de la interacción del caudal con la geomorfología de la sección del río intervenida (Boavida et al., 2015; Hauer et al., 2012, 2014; Parasiewicz et al., 1998; Tuhtan et al., 2012; Vanzo et al., 2016). En este marco postulamos que, el carácter de las zonas de procesos funcionales permite predecir, a grandes rasgos, aquellos procesos/mecanismos fluviales que serán activados o influenciados por la regulación de caudal. Es así como, en zonas con valle confinado, como es el caso de la zona de proceso funcional Sub-Andean, la regulación de caudal de tipo hydropeaking, tendrá una influencia mayor en la dimensión longitudinal y una limitada incidencia en la dimensión lateral, dado que el confinamiento del valle y ausencia de zonas de inundación limita la influencia de las variaciones de caudal a nivel lateral (Figura 6.11). En la dimensión longitudinal, la rápida liberación de agua sumada a la alta pendiente y confinamiento del valle producirán un aumento de la velocidad de corriente. Este incremento podría desencadenar deriva de carácter antropogénica (deriva catastrófica) de distintos subsidios alimenticios (menor tiempo de retención de alimento), sedimentos y organismos (Miller & Judson, 2014; Timusk et al., 2016). Por otro lado, se espera que, en aquellas horas del día con bajo caudal, y sobre todo en temporada estival, la profundidad del agua sea determinante en la calidad de las aguas en las zonas intervenidas, con aumentos de la temperatura y un descenso del oxígeno, lo cual podría ocasionar potenciales pérdidas de especies sensibles a estos cambios (ej. macroinvertebrados EPT; Rossel & de la Fuente, 2015; Kennedy et al., 2016). En las zonas de procesos funcionales ubicadas a una elevación intermedia como Central Valley Gravel Dominated y Central Valley Cobble Dominated, las variaciones de caudal tendrán influencia en las 3 dimensiones espaciales del río, longitudinal, vertical y lateral (Figura 6.12 y Figura 6.13). En Central Valley Gravel Dominated, esperamos que los mecanismos activados por la operación hydropeaking se diferencien acorde a los periodos sin operación (bajo caudal) o en periodo de operación (alto caudal). En la dimensión lateral se espera que el periodo de bajo caudal produzca desecación del lecho en la orilla del río, como también la ocurrencia de pozas desconectadas del curso principal. En la dimensión longitudinal se espera que los altos caudales inicien el proceso de deriva catastrófica impulsado por el aumento de la velocidad de corriente como por el transporte de sedimentos lecho del río. En esta zona, se espera que el transporte de sedimentos finos como arenas y así también de grava sea un proceso recurrente (Hauer et al., 2019). En Central Valley Cobble Dominated, se espera que los efectos del run-of-river estén asociados a dos instancias de la operación, uno asociado a la desviación de agua hacia las turbinas, dejando un tramo de río con bajos caudales, contrayendo el hábitat disponible. Mientras que, el otro a la liberación de agua, en tramos abajo de las turbinas, donde aumenta la variabilidad de los caudales, nivel de agua, profundidad (Almodüvar & Nicola, 1999; Anderson, 2017; Gibeau et al., 2016).

Nuestros resultados revelan que gran parte del curso principal y los principales ríos de la cuenca del río Biobío, se encuentran actualmente sometidos a caudales alterados producto de la operación de centrales hidroeléctricas. Por ello, es esperable que grandes áreas de la cuenca presenten cambios estructurales en su geomorfología a escala local (hábitat físico) y ecología. Todos estos impactos individuales generados por cada central hidroeléctrica instalada en esta cuenca derivan en impactos acumulativos a nivel de cuenca, con importantes implicancias en los ensambles de macroinvertebrados y peces a grandes escalas. En este contexto es esperable que los ensambles de macroinvertebrados y peces presenten reducción en sus abundancias a nivel de cuenca. Lo que, sin duda, convierte a esta cuenca en un sistema vulnerable en términos ecológicos.

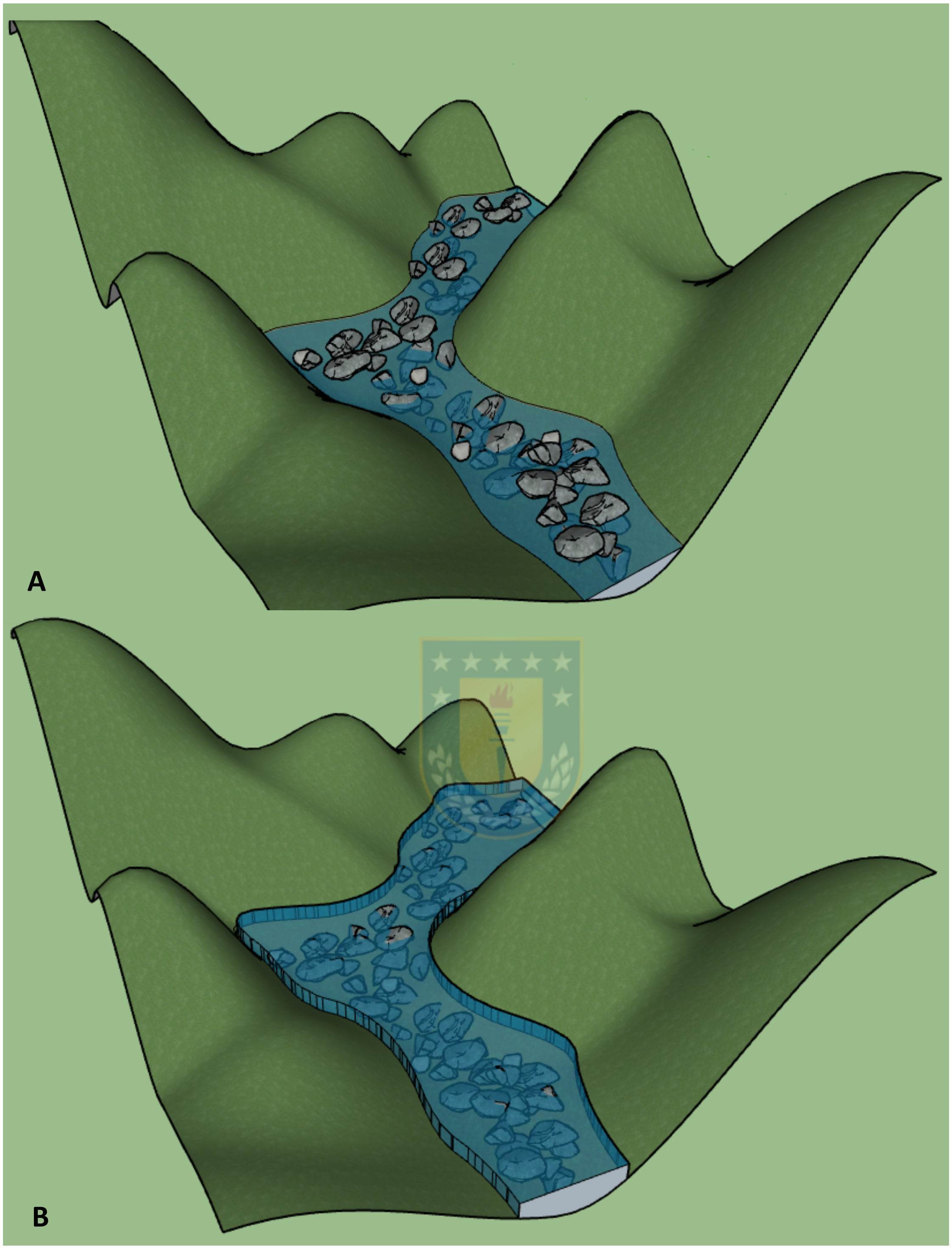

Figura 6.11. Representación diagramática de un tramo de río característico de una zona de proceso funcional llamada Sub-Andean en condiciones de variabilidad anual o diaria debido a hydropeacking, en que A) es bajo y B) es alto caudal.

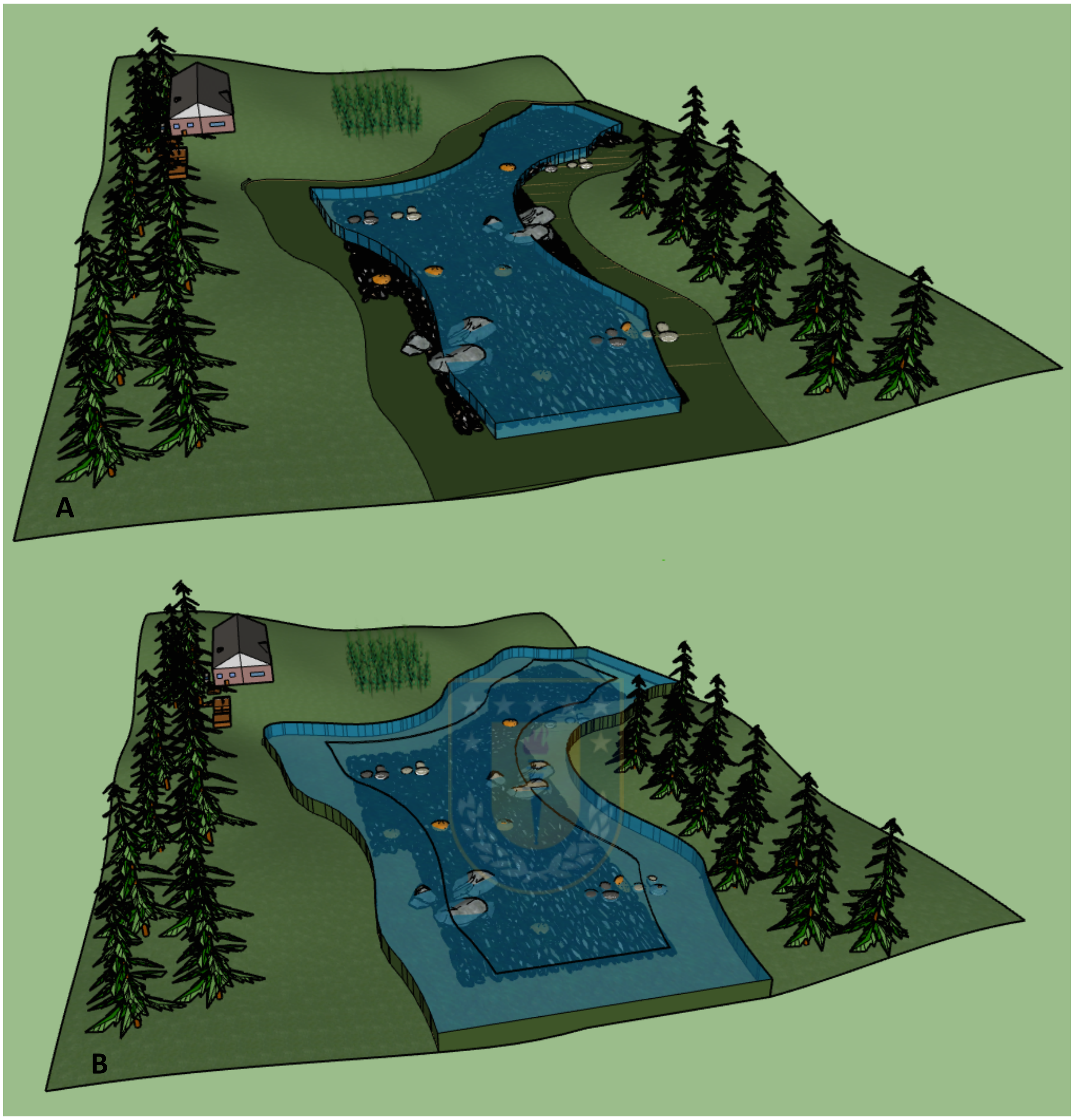

Figura 6.12. Representación diagramática de un tramo de río característico de una zona de proceso funcional denominada Central Valley Gravel Dominated en condiciones de variabilidad anual o diaria debido a hydropeacking, en que A) es bajo y B) es alto caudal.

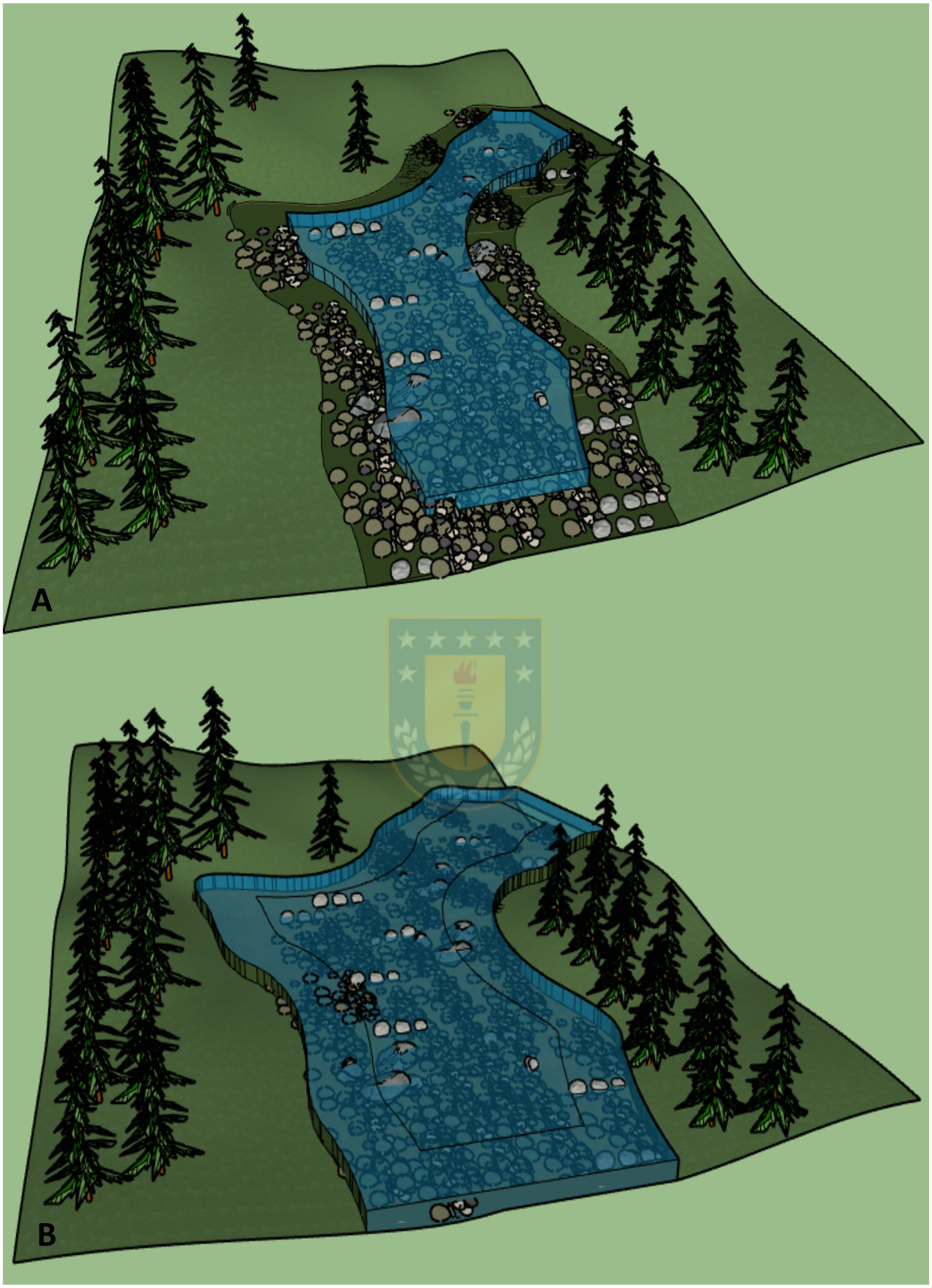

Figura 6.13. Representación diagramática de un tramo de río característico de una zona de proceso funcional denominada Central Valley Cobble Dominated en

condiciones de variabilidad anual o diaria debido a hydropeacking, en que A) es bajo y B) es alto caudal.

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7 Capítulo III. Interplay of geomorphology and hydrology drives macroinvertebrate assemblage responses to hydropeaking.

Este capítulo está basado en:

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7.1 Introduction.

Hydropeaking is a specific form of flow regulation representing a significant anthropogenic disturbance of rivers worldwide (Nilsson et al., 2005, Wang et al., 2019). The flow regime downstream of hydropeaking plants is characterised by rapid fluctuations in discharge and water levels during periods of hydropeaking peaking (cf. Tonolla et al., 2017). As a result, significant changes in hydraulic habitat occur in time periods of hours which can lead to permanent physical habitat modifications downstream such as changes in sediment composition and river channel morphology (cf. Hauer et al., 2014). These rapid environmental variations have negative effects on a range of aquatic organisms including fish (Casas-Mulet et al., 2014) and macroinvertebrates (Wang et al., 2019) among others.

The imposition of anthropogenic flow regimes triggers many ecosystem responses within river networks (Petts, 1986; Poff et al., 2010). However, flow driven biophysical processes occur at different hierarchical levels (Thorp et al., 2008). Thus, responses to flow alterations within river networks are inherently complex, where physical and ecological processes strongly interact, often in a non-linear manner (Phillips, 2010). In this way, larger-scale physical factors (i.e. flow history, fluvial zones) set the conditions within which smaller-scale factors operate (hydraulics, microhabitats; Thorp et al., 2008). Furthermore, responses occur within different time-scale, from hours to years (Bunn & Arthington, 2002; Vietz and Finlayson, 2017). Finally, the changes in ecological processes are transferred from individuals to populations and communities (Thorp et al., 2008).

Multidisciplinary approaches encompassing interplays of geomorphology, hydrology and ecology at a range of scales are required to unpack response complexities to natural and anthropogenic disturbances (Dollar et al., 2007, Thoms et al., 2007). Thorp et al. (2008) proposed a conceptual framework that serves as a tool to advance the understanding of rivers as hierarchical complex systems. This framework describes river networks as a set of fluvial zones that differ in physical character and spatial arrangement. These zones, called Functional Process Zones (FPZ), reflect variation in valley conditions, geological histories, discharge, and sediment regimes throughout the river network (Thorp et al., 2008). Substantial changes in the hydrological components that make up the flow regime could alter the attributes of an FPZ (Thorp et al., 2008). Consequently, it is expected that alterations of these attributes will affect biological components within FPZs and cause complex responses at different levels of their hierarchical organisation. Therefore, biological indicators used to monitor river network must match appropriate scales of geomorphological and hydrological processes. Thoms & Parsons (2002) and Meitzen et al., (2013) argue that the community level is an excellent indicator of the state of the river network, since it allows the detection of systematic changes and integrates responses from lower levels of biological organisation (population, individual). Furthermore, biological community level could be evaluated based on species´ taxonomy as well as their functional identity i.e. diversity of taxa in the community or functional guilds (groups of species that exploit the same class of environmental resources in a similar way; Simberloff & Dayan, 1991).

Macroinvertebrate assemblages are excellent indicators of the structure and functioning of river network (Bonada et al., 2006; Dos Santos et al., 2011). In addition, the composition of macroinvertebrates can reveal effects from anthropogenic disturbance, not detected by traditional assessments and display accumulative change of these in the time (Fierro et al., 2019). These characteristics make macroinvertebrate community assessment an efficient approximation of the ecological responses to environmental changes (Heino, 2004). Nowadays, two approaches are used in the macroinvertebrate research, one based taxonomic structure and other based in the functional trait characteristics of species in ecological communities. The first approach enable study the river from a perspective of species compositional where the identity of species has a principal role in the assessment (Example taxonomic families: Ephemeroptera, Plecoptera, Trichoptera). The second approach considers the function of these species in the rivers (Example; feeding guilds such as gatherers, shredders, scrapers, and filterers; Wallace & Webster, 1996).

Andean rivers in Chile are excellent systems to unpack the response of macroinvertebrate communities to flow alteration brought about by hydropeaking operations. These rivers are relatively short (<440 Km), with a high diversity of macroinvertebrates. These aquatic macroinvertebrates have high conservation value and are exposed to strong degradation and anthropogenic intervention such as hydropower plants (Figueroa et al., 2013; De los Rios, 2019). In this study, we aim to unpack the complex interplay of geomorphology and hydrology as drivers of macroinvertebrate assemblages in river network subjected to flow alteration. We determine the effects of hydropeaking on macroinvertebrate assemblage structure within the river network (in different FPZs). We hypothesized a significant effect of hydropeaking on the assemblage structure of macroinvertebrates at all ecological organisation level. Furthermore, we expected that this effect will differ between FPZs and to be primarily driven by geomorphic variables that operate at small spatial scale (e.g. river channel scale). Finally, hydropeaking affects shorter temporal-scale hydrological variables (i.e. daily and sub-daily) and, therefore, can be expected to have a significant effect on macroinvertebrate assemblages.

7.2 Methods

7.2.1 Study Area

This study was conducted in two Andean rivers located in central Chile; the Biobío (36° - 39° Lat. S; 24,260 km^2) and Imperial (37° - 38° Lat. S; 12,763 km^2). The Biobío and Imperial rivers represent typical Andean rivers in central Chile which are short (< 380 km in length), high energy (steep slopes), cobble-gravel bed river systems. Both river basins have a Mediterranean climate, with warm and dry summers, and cold and wet winters (Gasith & Resh, 1999). Annual rainfall varies from 1200 to 4000 mm in the Biobío River, and 1200 to 3000 mm in the Imperial River basin. Rainfall is higher in the Andean section of both basins and decreases with distance to the coastal regions. Hydrological regimes are pluvial (snow melt) and nival (rainfall) in the Biobío, and pluvial in the Imperial River. Variations in precipitation overtime result in high river flows in austral winter and spring and low flows in austral summer and autumn in both rivers. Furthermore, both these rivers are characterised by oligotrophic waters with low concentrations of nutrients (phosphorus <0,05 mg/L and nitrogen <0,4 mg/L) and suspended solids (<10 mg/L) and with conductivity lower than 120 µS, and pH being neutral to slightly alkaline (Parra et al., 1993).

Seven distinct Functional Process Zones (FPZs) – large tracts of the river network with distinct geomorphic character – occur in Biobío and Imperial river basin (Figure 7.1; Elgueta et al., 2019). Four FPZs are common to both rivers: The Sub-Andean (SA), Central Valley Cobble Dominated (CVCD), Central Valley Gravel Dominated (CVGD) and Lowland (Lo; Elgueta et al., 2019). Among these semi-confined SA FPZ characterised by high elevation (average 739 masl) and steep valley site slopes is the most abundant FPZ in the Biobío River basin and occurs more frequently in its upper Andean part. The Imperial River originates at the footsteps of the Andes and, therefore, SA FPZ is less frequent in its basin. CVGD FPZ characterised by low elevation (average 94 masl), open valley and sinuous channels is the most frequent FPZ in the Imperial River basin and second most frequent in the Biobío River basin (Elgueta et al., 2019).

Rivers in both basins are subjected to water developments. There are five hydropower dams in operation within the Biobío and these are located in two different FPZs (Figure 7.1). Three largest hydropower plants are located in the SA FPZs of the main river channel. These are, from upstream to downstream, the Ralco Dam (height (H) = 155 m; total volume (TV) = 1222 Mm3; operating since 2004), the Pangue Dam (H=113 m; TV = 175 Mm^3, operating since 1998) that directly affect SA FPZ, and the Angostura Dam (H=50 m; TV = 100 km^3, since 2013) that affects CVGD FPZ. In addition, there are two smaller hydropeaking dams in the Biobío Basin, and these are also located in SA FPZs (Duqueco tributary, H=15 m each, since 2007) but affect both SA FPZ and CVGD FPZ (Figure 7.1). Large section of the Biobío River remains unregulated. However, based on the presence of these dams, the Biobío River basin is highly fragmented (Fragmentation Index, FI = 0,436; Díaz et al., 2019), compared to the Imperial River basin characterised by a minimal level of fragmentation (FI: 0,002). There is only one run-of-river hydropower plant in the Imperial River that is located in a small tributary (Trueno stream – CVCD).

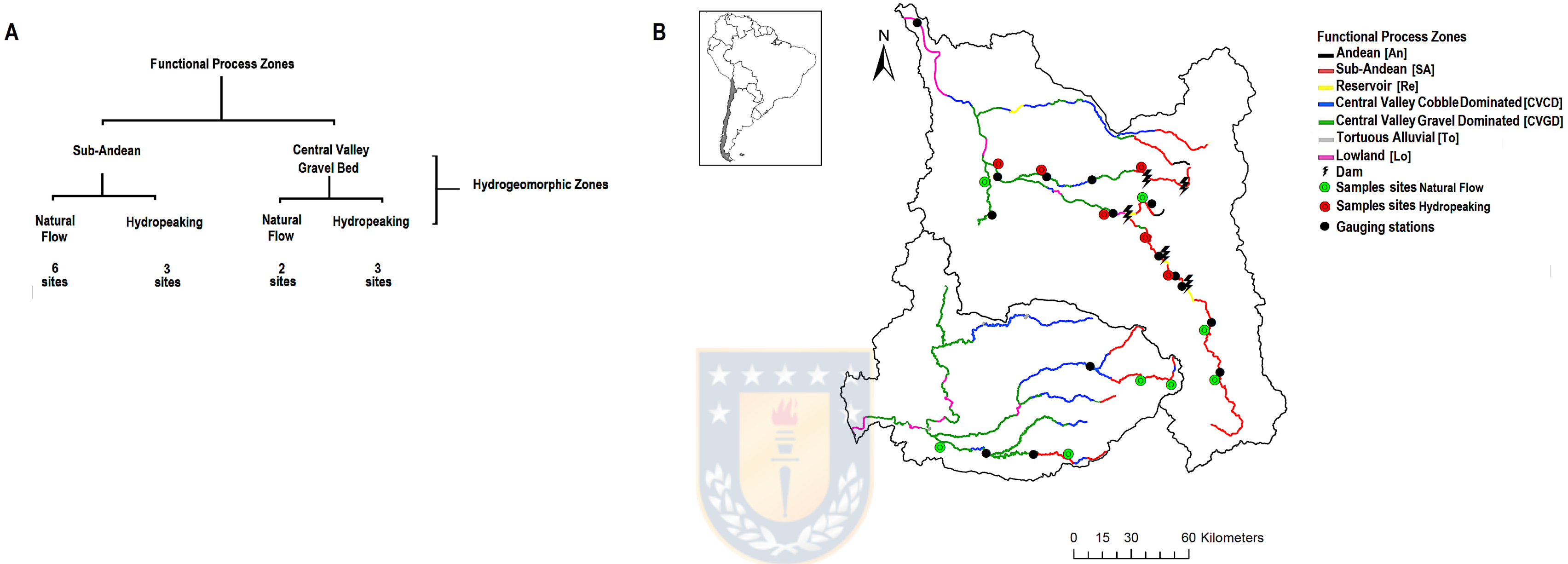

Figure 7.1. Study design (A) and study area (B) in the Biobío and Imperial River basins

Both the Biobío and Imperial river basins are located in the Chilean biodiversity hotspot with high endemism of fish and macroinvertebrate species (Myer et al., 2000; Dyer, 2000, Valdovinos, 2008). The Biobío River has the highest fish species richness in Chile, with a total of 18 native species, and 5 non-native species. Meanwhile, the Imperial River is inhabited by 15 native and 5 non-native species. Macroinvertebrate assemblages in both river basins are dominated by immature stages of aquatic insects (Valdovinos & Parra, 2006). Plecoptera (16 species), Diptera (15 species), Trichoptera (14 species), Ephemeroptera (12 species), and Coleoptera (12 species) are the dominant orders. Spatial distribution of benthic communities depends directly on type and stability of sediments (Valdovinos et al., 1993). In reaches with stable sediments such as those dominated by boulders, dominant taxa are insects (Trichoptera, Plecoptera, Ephemeroptera and Tipulidae) as well as Crustacean decapods (Aegla sp) and Molluscs (Ancylus, Chilina and Littoridina). In contrast, reaches with fine sediments are dominated by dipterans such as Chironomidae, Athericidae, Ceratopogonidae, Empididae, Limoniidae and Tipulidae. Annelids (Lumbriculis), Molluscs (Physa and Pisidium) and Crustaceans such as Gammaridae and Platyhelminthes (Dugesia) are also present.

7.2.2 Hierarchical study design

To unpack the complex responses to hydropeaking three hierarchically organised domains were recognised: geomorphology, hydrology, and ecology, in this study. The geomorphology domain was assessed at three spatial scales: catchment (3 variables), valley (7 variables) and river channel (5 variables; Table 7.1. Elgueta et al., 2019). The hydrology domain considered three temporal scales: long term (20 variables), daily (6 variables) and sub-daily (11 variables; Table 7.1. Appendix A). Finally, ecology domain considered macroinvertebrates assemblage structure (richness, abundance and diversity) at three ecological organizational levels: Overall taxa, Ephemeroptera – Plecoptera – Trichoptera (EPT) and specific feeding guilds (Predators, Gatherers, Shredders, Scrapers, Filterers).

To understand the effect of flow alteration on macroinvertebrate assemblages at the river network scale, sample sites were included in FPZs with a natural flow regime and a regulated flow (hydropeaking) regime. Sampling sites were located in two shared FPZs between the Biobío and Imperial river basins, the SA FPZ and CVGD FPZ (Figure 7.1). SA FPZ is typically located in headwaters and is characterised by high slopes (0,183 ± 0,07) and narrow valley widths (6428 m ± 4625 m; Elgueta et al., 2019). The river bed substratum of this FPZ is composed of boulders larger than 600 mm diameter with patches of smaller boulders (300-600 mm). Vegetation commonly extends from the valley to the riverbanks, providing inputs of detritus and wood from the riparian zone to the river. CVGD FPZ has lower slope (0,058 ± 0,05) and wider valley and floodplains (4421 m ± 5049 m; Elgueta et al., 2019). The river bed substratum is comprised of varying contributions of cobble, gravel, sand, and silt sized particles. Main inputs of nutrients and organic matter come from upstream and floodplains. The combination of FPZs and flow regimes categories determined four hydrogeomorphic zones: (1) natural flow (NF) in SA, (2) hydropeaking (HP) in SA, (3) NF in CVGD, and (4) HP in CVGD (Figure 7.1).

Table 7.1. Hydrological and geomorphic variables used to describe Functional Process Zones and Flow Regime Categories grouped by scale levels (time- scale for hydrology and spatial scale for geomorphology).

Geomophology Domain		**Hydrology Domain**	
Geomorphic variables	**Spatial Scale**	**Hydrological variables**	**Time - scale**
Elevation	Catchment	Sub-daily flow fluctuations	Sub-daily
Geology	Catchment	Flow-ramping rate	Sub-daily
Mean annual precipitacion	Catchment	Coefficient of variation of rise rate	Sub-daily
Valley width	Valley	Rise rate	Sub-daily
Valley trough width	Valley	Fall rate	Sub-daily
Ratio of valley to valley trough width	Valley	Coefficient of variation of fall and rising rate	Sub-daily
Left valley slope	Valley	Daily minimum	Sub-daily
Right valley slope	Valley	Daily maximum	Sub-daily
Down Valley slope	Valley	Daily delta	Sub-daily
Confinement	Valley	Daily standard deviation	Sub-daily
Channel belt wavelength	Channel	Reversals (falling and rising)	Sub-daily

Geomophology Domain		**Hydrology Domain**	
Geomorphic variables	**Spatial Scale**	**Hydrological variables**	**Time - scale**
Channel belt sinuosity	Channel	Variability in daily flows	Daily
Channel belt width	Channel	Mean daily flows	Daily
Number of channels	Channel	Median daily flows	Daily
River sinuosity	Channel	Skewness in daily flows	Daily
		Ranges in daily flows (10/90th), (25/75th)	Daily
		Spreads in daily flows (10/90th), (25/75th)	Daily
		Annual minima or maximum of 1-/3-/7-/30-/90-day means of daily discharge	Long-term
		Variability in annual minima or maximum of one-/3-/7-/30 /90-day means of daily discharge	Long-term

7.2.3 The flow regime – determination flow categories

Daily and sub-daily flow data for both rivers were obtained from the General Directorate of Water (DGA) of the Chilean Ministry of Public Works. Flow data for period greater than 30 years were available for 15 gauging stations throughout both river networks. For each station, 41 hydrological variables representing the magnitude, frequency, duration, seasonality, and variability of the flow regime were estimated (cf. Richter et al., 1996; Meile et al., 2009; Bevelhimer et al., 2015). These variables characterised the long term (annual), daily and sub-daily components of the flow regime at each gauging station. The 15 gauging stations were grouped into two flow regime categories. Those corresponding to a natural flow regime (i.e. not influenced by upstream dams or water resource development – natural flow (NF). The second group were those subject to strong changes the magnitude, frequency and duration of flow to sub-daily, daily and monthly time scale because of the influence of hydropower dams (with a high reservoir volume to discharge inflow ratios), and where dam operations are designed to meet sub-daily power generation demands (hydropeaking group; HP). Differences in the flow character of the two flow categories – NF and HP – were assessed by permutational analysis of variance (PERMANOVA; Anderson, 2017).

7.2.4 Macroinvertebrates sampling

Macroinvertebrates were sampled at a total of 14 sites distributed in four FPZs shared between the two river basins: SA-NF (6 sites), SA-HP (3 sites), CVGD-NF (2 sites) and CVGD-HP (3 sites; Figure 7.1). Benthic macroinvertebrates were sampled using a surber sampler (0.09 m2, 500 µm mesh size). Six samples were collected randomly at each site at depth less than 60 cm. Material collected in each sample was preserved in the field in 95% ethanol. In the laboratory, the total of macroinvertebrates in each sample was separated using a dissecting microscope. Each individual collected was identified to the lowest taxonomic level (genus or family for aquatic insects) based on Dominguez & Fernandez (2009), and classified in one of five functional feeding guilds – predators, gatherers, shredders, scrapers, filterers – according to Merrit & Cummins (2006), Miserendino & Pizzolon (2003) and Pérez et al. (2004).

7.2.5 Statistical analyses of macroinvertebrate assemblages

To investigate the effects of the two flow regimes (NF and HP), FPZs (SA and CVGD) and hydrogeomorphic zones (SA-NF, SA-HP, CVGD-NF and CVGD-NF) on the macroinvertebrate assemblage structures, we used a permutational multivariate analysis of variance based on abundance data (PERMANOVA). Data were log10(x + 1) transformed, and Bray–Curtis index (Bray & Curtis, 1957) was used as the dissimilarity measure for PERMANOVA. The Index of Multivariate Dispersion was also calculated to determine the variance of each macroinvertebrate community at the 14 sites (IMD; Warwick & Clarke 1993). IMD values were compared among flow categories, FPZs and hydrogeomorphic zones. The "natural variability" of each macroinvertebrate assemblage within each FPZ was estimated based on data from sites with natural flow (no hydropeaking). Diversity was also assessed using the Shannon diversity index (H'; Shannon & Weaver, 1949). Comparisons among flow categories, functional process zones and hydrogeomorphic zones were performed using one-way analysis of variance (ANOVA) for overall macroinvertebrates, EPT, and feeding guilds (predators, gatherers, shredders, scrapers, filterers).

7.2.6 Environmental drivers of macroinvertebrate assemblages

Associations among environmental drivers and macroinvertebrate abundances among different domain were analysed using distance-based linear modelling (DISTLM) with stepwise variable selection using adjusted R^2 criterion selection procedure run with 9999 permutations (Anderson, 2001; McArdle & Anderson, 2001). DISTLM is a multiple multivariate regression analysis that uses permutation to test for the strength and significance of relationships between predictor (i.e. hydrological and geomorphological variables at different spatial and temporal scales) and ecological variables (i.e. assemblage structure at a given ecological organisation level). Subsequently, proportion of significant variables with a proportion of the variation above 90th percentile based on marginal tests was calculated for each domain and scale category (catchment, valley, river channel for geomorphologic variables and long-term, daily and sub-daily for hydrological variables).

7.3 Results

7.3.1 Flow regime categories

Significant differences were observed between the two flow regime categories: natural flow (NF) and hydropeaking (HP, PERMANOVA, pseudo-F: 13,47 $p<0.001$). The natural flow regime is characterised by a low variation of magnitude, frequency and rate of change in flow at sub-daily and daily time-scales. By comparison, the hydropeaking flow regime category is characterised by a high variation in the magnitude, frequency and duration components of the flow regime at the sub-daily, daily and monthly time-scales. Mean daily difference in flow in the natural flow regime category was 11 m^3/s, whereas it reached up to 156 m^3/s in the hydropeaking flow category (appendix B). Thus, the hydropeaking flow regime is more variable over an extended range of time scales – sub daily to monthly – compared to the natural flow regime.

7.3.2 Macroinvertebrate assemblage composition and structure

A total of 80 taxa were identified in the Biobío and the Imperial river basins. 54 taxa were identified at the genus level, 23 at the family level and three at higher taxonomic categories (Phylum, Class or Order; Table 7.2). Macroinvertebrate assemblages were composed mainly of insects, then crustaceans, followed by molluscs. 46 macroinvertebrate taxa composed the EPT group. Taxa were distributed in 5 feeding guilds (13 taxa were shredders, 27 predators, 10 scrapers, 3 filterers and 27 gatherers, Table 7.2). No significant difference in total macroinvertebrate abundance was observed between the two FPZs with a NF but EPTs, gatherers, shredders were significantly more abundant in the SA FPZ compared to the CVGD FPZ. However, filters and scrapers were more abundant in the latter (

Table 7.4). When all taxa were considered, richness at sites with natural flow was higher in SA FPZ (64 species) compared to CVGD FPZ (37 species; Appendix C). In addition, species richness was significantly higher at the NF sites compared to HP for overall macroinvertebrates and shredders in SA FPZ, and filterers in CVGD FPZ (Table 7.3). In general, macroinvertebrate abundance was significantly higher in sites with a natural flow regime compared to sites subjected to hydropeaking in both FPZs and for most of the macroinvertebrate assemblage organisation levels (Figure 7.2, Table 4; Appendix D). These differences were most evident for shredders in SA FPZ and filterers in CVGD FPZ with mean abundances in NF about 5-fold and 13-fold higher compared to HP, respectively (Figure 7.2,

Table 7.4). An opposite trend was observed for scrapers in CVGD with abundances higher in HP sites compared to NF sites. There were no significant differences in macroinvertebrate diversity (H´) between hydrogeomorphic groups for most ecological organisation levels (Appendix D).

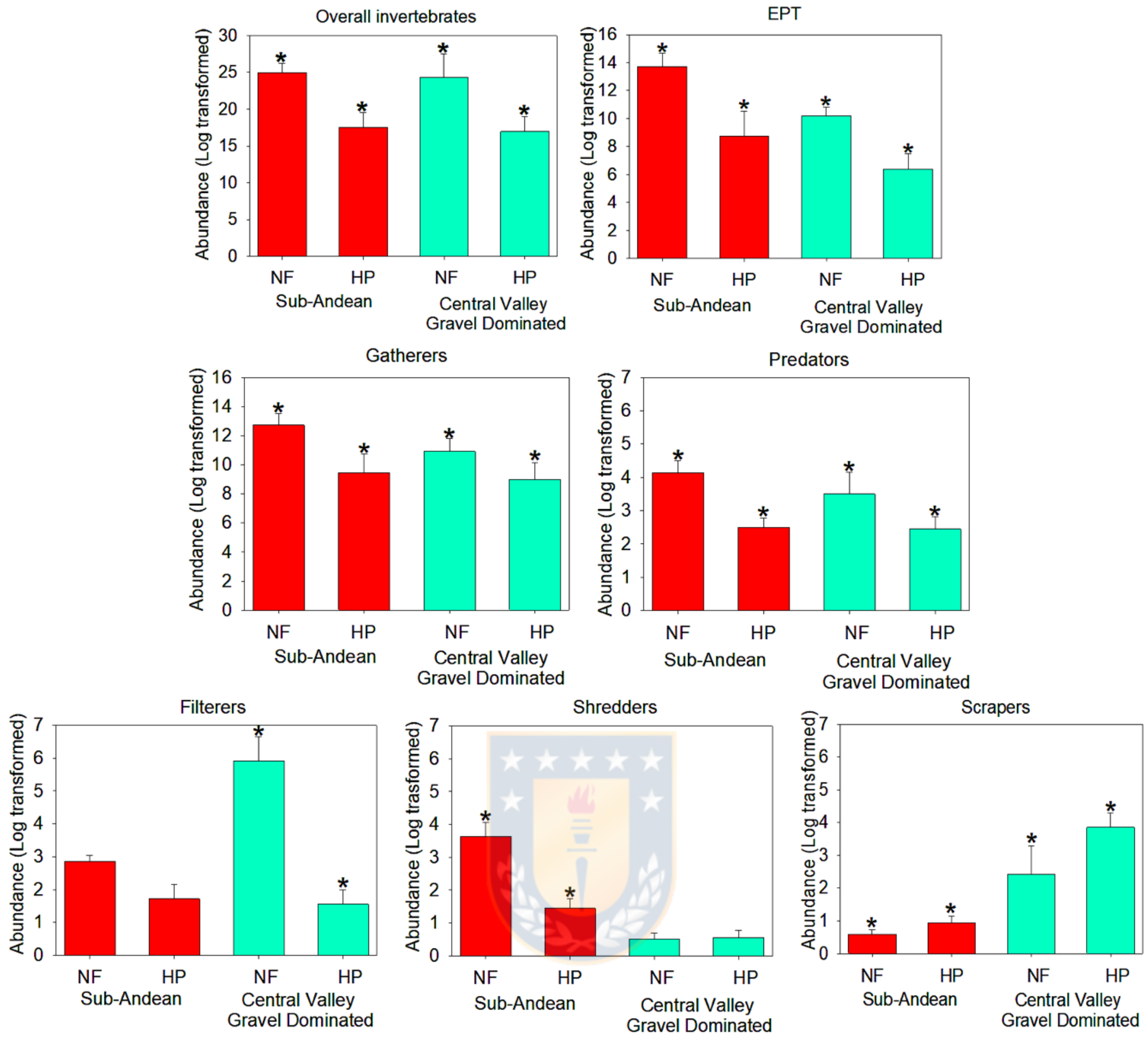

Figure 7.2. Comparison of macroinvertebrate abundances (Log(X+1) transformation) at different levels of ecological organisation between hydrogeomorphic zones. Natural flow, NF; Hydropeaking, HP. Mean and Standard Error. * p<0,05 based on PERMANOVA (see Table 7.3).

The variance in abundance of macroinvertebrate assemblages (measured as index of multivariate dispersion) was markedly different between the two FPZs. This was dependent on the ecological level of organisation as well as the total invertebrate assemblage. EPT as well as gatherers and filterers had a higher IMD in the SA FPZ while predators and shredders had a higher IMD in the CVGD FPZ. Furthermore, the variance was substantially higher in hydropeaking sites compared to natural flow sites for all ecological organisation levels except for scrapers (Figure 7.3). The variance response to flow regulation also varied between the hydro-geomorphic areas. All ecological levels except scrapers had a higher IMD in the hydropeaking sections of the SA FPZ while most of the ecological levels had a higher IMD in those sections of the CVGD FPZ – shredders and filters were the exception having a higher IMD in the natural flow sections of the CVGD FPZ.

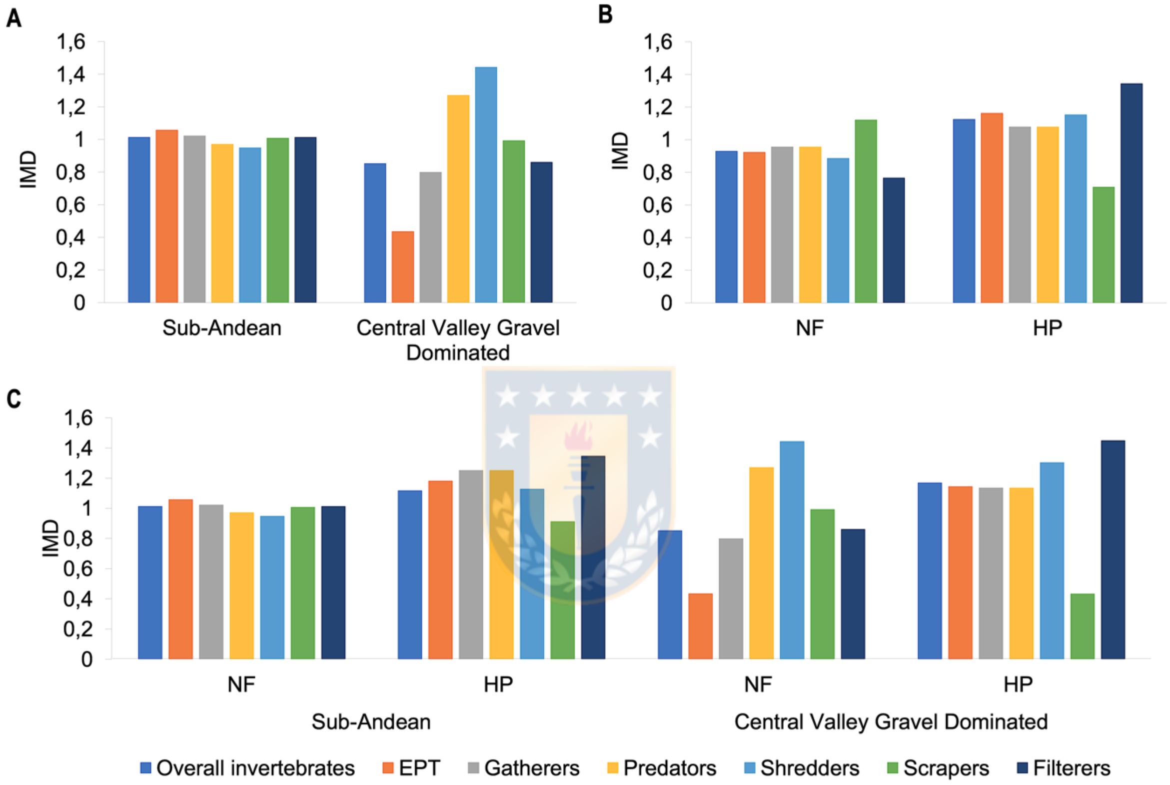

Figure 7.3. Variance (Index of Multivariate Dispersion Index, IMD) of macroinvertebrate abundances at different levels of ecological organisation for (A) Flow Regime Categories (Natural flow, NF; Hydropeaking, HP), (B) Functional Process Zones and (C) Hydrogeomorphic Zones.

Table 7.2. List of species and functional feeding guilds

Feeding guild	**Order**	**Family**	**Taxa**
Predators	Ephemeroptera	Ameletopsidae	*Chaquihua sp*
			Chiloporter eatoni
	Trichoptera	Hydrobiosidae	Hydrobiosidae
		Philorheitrhidae	Philorheitrhridae
	Decapoda	Aeglidae	*Aegla abtao*
			Aegla araucaniensis
			Aegla pewenchae
	Diptera	Athericidae	Athericidae
		Ceratopogonidae	Ceratopogonidae
		Empididae	Empididae
		Ceratopogonidae	*Forcipomyia sp*
		Limoniidae	*Limonia sp*
		Tipulidae	Tipulidae
	Coleoptera	Hydrophilidae	Hydrophilidae
		Dytiscidae	Dytiscidae
		Gyrinidae	Gyrinidae
		Hydraenidae	Hydraenidae
	Hemiptera	Gerridae	Gerridae
		-	Hemiptera
	Annelida	Hirudinidae	Hirudinidae

Feeding guild	**Order**	**Family**	**Taxa**
	Trombidiformes	-	Hydracarina
	Mecoptera	Nannochoristidae	*Nanochorista sp*
	Nematoda	-	Nematoda
	Odonata	Gomphidae	*Neogomphus sp*
	Megaloptera	Corydalidae	*Protochauliodes sp*
	Araneae	-	Araneae
	Turbellaria	-	*Temnocephala sp*
Gatherers	Ephemeroptera	Baetidae	*Americabaetis sp*
			Andesiops ardua
			Andesiops peruvianus
			Andesiops torrens
			Camelobaetedius sp
		Caenidae	*Caenis chilensis*
		Leptophlebiidae	*Hapsiphlebia anastomosis*
			Leptophlebiidae
			Meridialaris chiloense
			Meridialaris diguillina
			Meridialaris laminata
			Meridialaris sp
			Nousia crena
			Nousia maculata
			Nousia minor

Feeding guild	**Order**	**Family**	**Taxa**
			Penaphlebia chilensis
			Penaphlebia sp
			Penaphlebia vinosa
			Rhigotopus sp
		Onicigastridae	*Siphlonella guttata*
	Trichoptera	Hydroptilidae	*Metrichia sp*
		Hydroptilidae	*Oxyethira sp*
	Diptera	Chironomidae	Chironomidae
		Psychodidae	Psychodidae
	Coleoptera	Elmidae	Elmidae
		Staphylinidae	Staphylinidae
	Amphipoda	Hyaleliidae	*Hyalella* sp
Shredders	Plecoptera	Grypopterigidae	*Antarctoperla michaelseni*
			Aubertoperla sp
			Ceratoperla sp
			Chilenoperla brundini
			Klapopteryx armillata
			Klapopteryx kuscheli
			Limnoperla jaffueli
			Notoperlopsis femina
			Pelurgoperla personata
			Penturoperla barbata

Feeding guild	Order	Family	Taxa
		Perlidae	*Neuroperlopsis patris*
			Diamphipnoa helgae
			Diamphipnopsis samali
	Trichoptera	Sericostomatidae	*Sericostomatidae*
Scrapers	Trichoptera	Leptoceridae	Leptoceridae
		Glossosomatidae	Glossosomatidae
	Gastropoda	Siphonoridae	*Chilina dombeyana*
		Amnicolidae	*Littoridina cummingi*
		Physidae	*Physa chilensis*
		Ancylidae	*Uncancylus sp*
	Hemiptera	Corixidae	Corixidae
	Coleoptera	Psephenidae	*Tychepsephenus felix*
	Plecoptera	Notonemuridae	*Udamocercia sp*
Filterers	Sphaeriida	Sphaeriidae	*Pisidium sp*
	Diptera	Simuliidae	Simuliidae
	Trichoptera	Hydropsychidae	*Smicridea sp*

Table 7.3. Differences in macroinvertebrate assemblages (Species richness) among hydrogeomorphic zones (Flow regime categories combined with functional process zones) for the Biobío and Imperial rivers. Kruskall-Wallis results are provided for all invertebrate, shredders and filterers.

Functional process zone	**Ecological organization**	**NF vs HP**		
		N	**H**	**p**
Sub-Andean	Overall	84	14,15687	0,0027
	Shredders	84	37,37572	0,000
Central Valley Gravel Dominated	Filterers	84	27,66417	0,000

Table 7.4. Differences in macroinvertebrate assemblages (Bray–Curtis dissimilarity based on abundances) among hydrogeomorphic zones (Flow regime categories combined with functional process zones) for the Biobío and Imperial rivers. PERMANOVA results are provided for all invertebrate, EPT groups and functional guilds.

Feeding guilds	**Sub-Andean**		**Central Valley Gravel Dominated**	
	Pseudo-F	**P**	**Pseudo-F**	**P**
Overall invertebrates	3,825	**0,0006**	5,047	**0,0002**
EPT	6,429	**0,0002**	4,095	**0,0001**
Predatos	3,616	**0,0001**	2,004	**0,0491**
Gatherers	4,908	**0,0001**	2,692	**0,0283**
Shredders	4,008	**0,0025**	1,302	0,2710
Scrapers	2,714	**0,0365**	6,059	**0,0004**
Filterers	2,578	0,0899	4,162	**0,0061**

7.3.3 Macroinvertebrate assemblage driver responses

The interactive effects of hydrology and geomorphology were evident at all ecological organization levels (Figure 7.4; Appendix E) in both FPZs. In the SA FPZ, sub-daily hydrological variables were the most dominant drivers of macroinvertebrate assemblages (ie. significance ratio >0.75). By comparison, a combination of hydrology and geomorphology variables were dominant in the CVGD FPZ, whereas long term variables had little significance in both FPZs. Furthermore, river valley geomorphic variables also played significant role in both FPZs. In addition, catchment scale geomorphic variables influenced macroinvertebrate assemblages of some of the ecological organization levels in the CVGD FPZ (overall macroinvertebrates, EPT and gatherers). In contrast, river reach scale geomorphic variables played little importance as drivers of macroinvertebrate assemblages in SA FPZ.

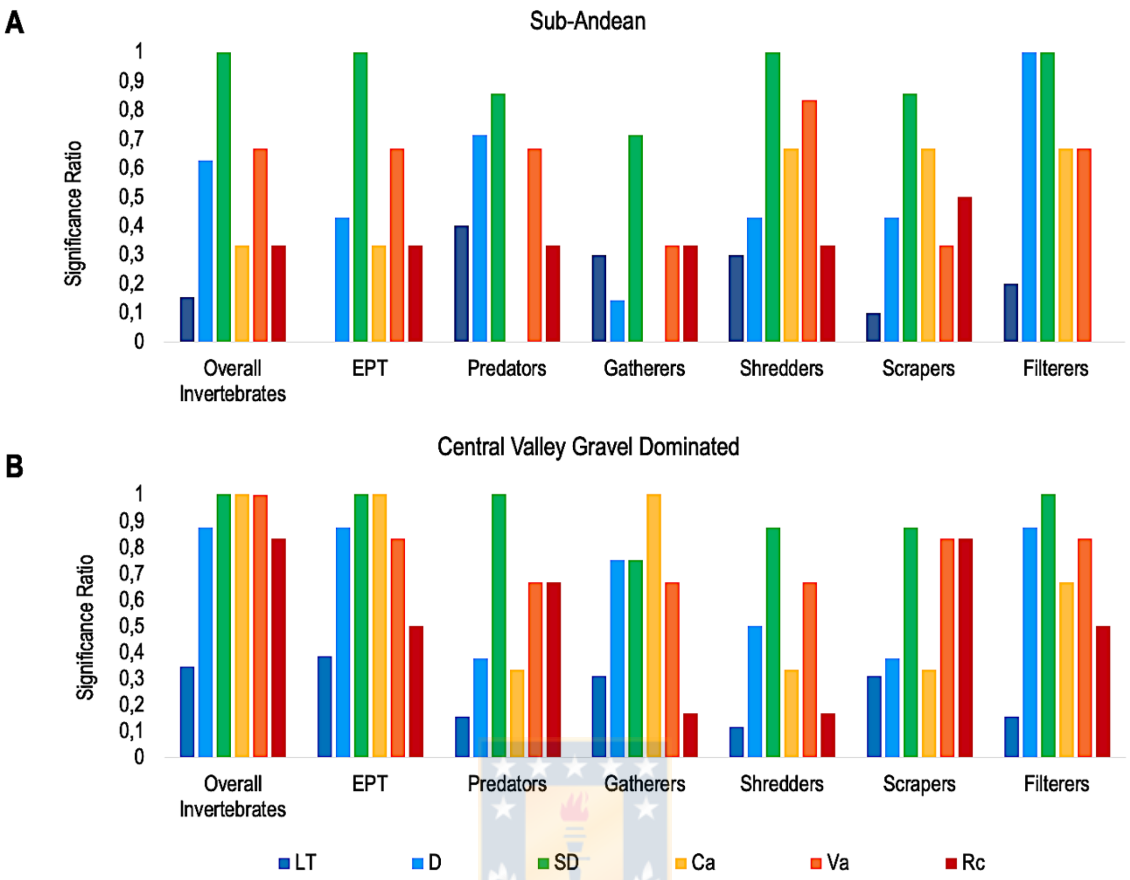

Figure 7.4. Hydrological (LT: Long-time, D: Daily, SD: Sub-daily) and geomorphological (Ca: Catchment, Va: Valley, Rc: River Channel) drivers of invertebrate assemblage structure at different levels of ecological organization for Sub-Andean (A) and Central Valley Gravel Dominated (B). Significance ratio represents the proportion of significant hydrological and geomorphological variables to the total number of variables used within each hierarchical level.

7.4 Discussion

A significant effect of hydropeaking on macroinvertebrate assemblage structure was documented in this study of Andean high energy rivers. The abundance of macroinvertebrates was lower in sites with hydropeaking and this effect was consistent across FPZs. This reduction was evident across all ecological organisation levels. The only exception were scrapers, which showed an increase in abundance at sites with hydropeaking. In addition, the variance of macroinvertebrate abundances was significantly higher in hydropeaking sites in both FPZs. This increase in the variance of assemblages in response to hydropeaking was the strongest for filterers. Scrapers were the only exception also here and have shown lower variance in hydropeaking sites compared to natural flow regime sites. Overall, this study of macroinvertebrate assemblage structure in two high-energy Chilean river systems adds to global database of river ecosystem response to hydropeaking-induced flow alterations. Those in the USA have dominated studies of the effects of dams on macroinvertebrates (cf. Wang et al., 2019). Attempts to build general river ecosystem response models to flow regulation require data from an increased geographical base, like Chile, because of regional differences in eco-hydro-geomorphology, biological communities, and nonlinear interactions between the two (Habit et al., 2018).

Many studies have shown the role of environmental filters in determining community composition and functional organization of aquatic communities in river systems and their response to anthropogenic disturbances (e.g., Astorga et al., 2011; DeBoer et al 2020). Our results not only support the conclusion that FPZs are an appropriate scale to study macroinvertebrate taxonomic composition and functional organization within river networks but also, they are the product of multiple-scale habitat filters. In both FPZs (i.e., SA and CVGD) hydrogeomorphic variables had a strong influence on the community composition. This observation is similar to that reported by Maasri et al., (2019), in rivers of the Mongolian plateau. However, marked differences in the influence of hydrogeomorphic variables, operating at different scales, on macroinvertebrate communities occurred for two FPZs in the Biobío River basin.

Sub-daily components of the flow regime were the dominant filtering pressure on communities of the SA FPZs. By comparison, geomorphic variables at catchment, valley and river channel scale along with Daily flow regime components increased in prominence in the CVGD FPZ. In addition, the response of macro invertebrates to hydropeaking also differed between the two FPZs and this was most notable in the variance of assemblages. In the SA FPZ there was a general trend for variance to increase whilst in the CVGD FPZ the variance response to hydropeaking was variable, with predators, shredders and scrapers all decreasing in variance. Thus, the resilience of FPZs to imposed hydropeaking flow regimes may differ i.e. vary in their ability to absorb altered flow regimes and retain a similar structure, function and set of feedbacks.

The development of hydropower plants has significantly altered the downstream flow regimes in the two Chilean Andean river systems. Similar effects were reported in other river systems in North America and Europe (Zimmerman et al., 2010; Carolli et al., 2015; Chen et al., 2015; Melcher, et al 2016; Bejarano et al., 2017; Ashraf et al., 2018; Hecht et al., 2019). Hydropeaking severely affected hydrological variables that describe flow regime at daily and sub-daily temporal scales. Specifically, variability of daily flow, sub-daily flow fluctuation and sub-daily flow ramping rate significantly increased at hydropeaking sites. These hydropeaking driven alterations of the flow regime caused significant changes in macroinvertebrate assemblages. Furthermore, these alterations were modulated by geomorphology and responses differed between FPZs.

Possible mechanisms that could explain decreases in the abundance of macroinvertebrates in the Biobío River relate to downstream drift, physical habitat and water quality alterations as well as food availability changes (Bunn & Arthington, 2002; Brooks et al., 2018; Wang et al., 2019). Hydropeaking induced catastrophic drift has been previously documented and is expected to affect macroinvertebrates across all ecological organization levels (Moog, 1993; Céréghino & Lavandier, 1998; Céréghino et al., 2002; Bruno et al., 2013; Schülting et al., 2016; Schülting et al., 2018). A previous study in the Biobío River has shown that hydropeaking related discharge peak caused significant macroinvertebrate drift and the abundance of drifting macroinvertebrates was directly proportional to macroinvertebrate abundance in benthic habitats at corresponding sampling sites (García, 2011). Furthermore, catastrophic drift may also be caused by sediment mobilization as shown in other river systems (Gibbins et al 2007; Schülting et al 2016, 2018; Vericat et al., 2020). In addition to macroinvertebrate drift caused by the direct effect of higher water velocities and sediment mobilization, abrupt water temperature changes also cause significant increase of downstream drift frequency (Carolli et al., 2012). The effects of water temperature changes are expected to be significant especially for EPT (Bruno et al., 2013, Li et al., 2013).

Direct physical habitat changes effect macroinvertebrate abundances in river reaches subject to hydropeaking (Cabaltica et al., 2013). Hydropeaking can result in successive daily dewatering of the river shoreline (Theodoropoulos et al., 2015; Melcher et al 2017). This dewatering exposes macroinvertebrates to desiccation and asphyxia that will have direct consequences in their population abundances (Moog et a., 2003; Valentin et al., 2006, Theodoropoulos et al., 2015). Furthermore, dewatering also exposes eggs to desiccation and damage due to direct solar radiation as previously shown for EPT (Kennedy et al., 2016; Poff & Schmidt 2016). Hydropeaking also causes sediment coarsening due to flushing of fine sediments (Petts, 1984; Vericat et al., 2020). This sediment coarsening increases catastrophic drift probability of macroinvertebrates (Gomi et al., 2010).

Hydropeaking results in rapid water level fluctuations, which induce water quality changes that cause macroinvertebrate abundance declines (Calapez et al 2018). Temperature changes caused by hydropeaking have been shown to affect life-histories of various EPT species that led to abundance declines (Hynes, 1976; Brittain, 1988; Saltveit and Brittain, 1987; Calapez et al 2018). Hydropeaking causes significant temperature increase and decrease of concentration of oxygen in pools that are formed during daily low water conditions (Rolls et al., 2012). Due to altered temperature and oxygen conditions these pools are unsuitable as a refuge for highly intolerant to high temperatures and hypoxia EPT families (Tierno de Figueroa et al., 2010; Saari et al., 2017; Pedreros et al., 2020). Furthermore, hydropeaking is causing significant decrease in dissolved oxygen concentrations that cause decrease of abundances of gill-breathing macroinvertebrates that in our study are mostly represented by the EPT, as well as shredders and gatherers among feeding guilds (Calapez et al 2018). Furthermore, increased amount of suspended sediments during peak discharges may cause damage to fragile feeding devices of filterers that are sensible to abrasion (Moog et al 1993; Englund & Malmqvist, 1996).

Apart from direct damage to feeding devices, hydropeaking also affects various macroinvertebrate groups by significantly changing their food availability (Troelstrup & Hergender, 1990). Shredders, for example, strongly depend on the availability of leaf litter as food. Hydropeaking leads to instability of leaf litter and have been previously shown to cause reduction in abundances of shredders (Schade and Fisher, 1997, Casas et al., 2000). The abundance declines of prey species due to food availability changes as well as catastrophic drift, habitat and water quality changes is expected to also cause significant decreases of abundances of predators (Englund and Malmqvist, 1996).

In contrast, water velocity and quality changes caused by hydropeaking seem to give advantage to scrapers that showed significant increase of abundances and decrease of variances in parts of river network that are influenced by hydropeaking. Snails such as Chilina dombeyana (Bruguiere 1789) dominated scraper assemblages at all sites. Indeed, these snails have ability to breathe oxygen directly from the atmosphere and can retreat into their shells using their operculum, seal the shell and remain tightly attached to the substrate during periods of environmental stress such as high water velocities or desiccation (Thorp and Covich, 1991; Vinson, 2001, Collier, 2014; Kennedy et al., 2016). Even though, abundances of scrapers significantly increased as a response to hydropeaking in both FPZs, this response was stronger in CVGD FPZ due to significantly higher abundances of scrapers in this FPZ.

This study of two Andean high energy river systems provide evidence that hydrological variables at sub-daily temporal scales are primary drivers of macroinvertebrate assemblage structure level in river systems affected by hydropeaking. Furthermore, changes in macroinvertebrate assemblages induced by hydropeaking sub-daily flow variation were visible at all ecological organization and consistent within the river network (among FPZ). Indeed, hydropeaking induced sub-daily flow variability has been suggested to affect various ecological processes (Bevelhimer et al 2014; Chen et al., 2015, Giulivo et al., 2019), but empirical evidence of specific mechanisms of these effects is scarce. We show how macroinvertebrate assemblage structure responds to sub-daily flow variability that induces habitat characteristics to which most riverine macroinvertebrates are not adapted (Southwood et al., 1977; Cushman, 1985). In contrast to what was expected, river channel scale variables were not significant as driver of macroinvertebrate assemblage structure in both FPZ. As such, among geomorphological variables river valley scale variables appeared to determine macroinvertebrate assemblage structure in both FPZ.

This study elucidates scales of impact of hydropeaking flow management on structure of macroinvertebrate assemblages across ecological organisation levels and large tracts of the river network with distinct geomorphic character (FPZs). As such, we demonstrate the effects of hydrological variables at sub-daily (micro) temporal scale but geomorphic variables at valley (meso) spatial scale across river network. Therefore, to minimize the effects of hydropeaking on macroinvertebrate assemblages, flow management should consider reduction of sub-daily variability. Furthermore, macroinvertebrate assemblages that characterize confined zones within the river network seem to be more resilient to hydropeaking that those inhabiting open valley zones. As such, placement of new barriers should consider not only their position within the river network but also their effects downstream that strongly depend on characteristics of river valley.

7.5 Ackowledgements

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Appendix A.

Table A.1. Hydrological variables used to characterise the flow regime of the Biobío and Imperial rivers. Sub-daily (SD), daily (D), long time (LT).

Hydrological variable	Time-scale	Description
Sub-daily flow fluctuations	SD	Difference between the maximum and the minimum daily discharge. This value is normalized by the mean daily discharge to account for differences in river and catchment scales.
Flow-ramping rate	SD	Change in discharge between two successive discharge observations divided by the observation time interval.
Coefficient of variation of rise rate	SD	Rise rate divided by median daily flow.
Rise rate	SD	Average rate of positive changes in flow from one day to the next divided by median daily flow.
Fall rate	SD	Average rate of negative changes in flow from one day to the next divided by median daily flow.
Coefficient of variation of fall and rising rate	SD	Fall rate or rise rate divided by median daily flow.
Daily minimum	SD	Lowest measured flow during a 24-h period (Qmin).
Daily maximum	SD	Highest measured flow during a 24-h period (Qmax).
Daily delta	SD	Difference between daily minimum and daily maximum represents the amount of daily flow change.
Daily standard deviation	SD	The common statistical calculation of the 24-hourly flow values.
Reversals (falling and rising)	SD	Number of changes between rising and falling periods of the hydrograph; adapted from a similar metric derived with daily data (Richter et al., 1996; TNC, 2007).
Variability in daily flows	D	Daily flow averages for each year and then averaged across years.

Hydrological variable	**Time-scale**	**Description**
Mean daily flows	D	Mean daily flow.
Median daily flows	D	Median daily flow.
Skewness in daily flows	D	Mean daily flows divided by median daily flows.
Ranges in daily flows (10/90th), (25/75th)	D	Ratio of 10th/90th and 25th/75th percentiles in daily flows overall years.
Spreads in daily flows (10/90th), (25/75th)	D	Ranges in daily flows divided by median daily flows.
Annual minima or maximum of 1-/3-/7-/30-/90-day means of daily discharge	LT	Magnitude of minimum or maximum annual flow of various duration, ranging from daily to seasonal (Low and high flow)
Variability in annual minima or maximum of 1-/3-/7-/30 /90-day means of daily discharge	LT	Coefficient of variation of annual minima or maximum of 1-/3-/7-/30-/90-day divided by means of daily discharge (Low and high flow).

Appendix B.

Table B.1. Mean and standard deviations of hydrological variables by flow regime categories (NF, HP) and functional process zones (SA: Sub-Andean; CVGD, Central Valley Gravel Dominated) for the Biobío and Imperial rivers.

Hydrological Variables	**SA**				**CVGD**			
	NF		**HP**		**NF**		**HP**	
	Mean	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**
Sub-daily flow fluctuations	0,12	0,04	0,97	0,26	0,10	0,00	0,50	0,08
Flow-ramping rate (minima)	0,00	0,00	0,33	0,46	0,00	0,00	1,06	1,50
Flow-ramping rate (maximum)	2,67	1,87	125,27	65,41	4,19	2,48	60,82	65,60
Coefficient of variation of rise rate	0,06	0,08	47,58	26,52	0,22	0,30	15,37	18,89
Rise rate falling	4,79	4,68	44,48	33,92	12,21	15,73	10,95	11,22
Rise rate rising	3,17	1,34	39,77	27,90	5,53	5,28	11,17	9,81
Coefficient of variation of falling rate	1,89	0,77	1,60	0,29	1,68	0,61	1,55	0,71

Hydrological Variables	SA				CVGD			
	NF		HP		NF		HP	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Coefficient of variation of rising rate	2,04	0,93	1,50	0,34	1,99	0,93	1,95	0,18
Daily minimum	56,90	43,20	139,26	68,64	62,23	11,41	194,24	231,59
Daily maximum	66,95	47,56	325,69	155,51	74,09	14,50	309,06	359,12
Daily delta	10,05	4,80	176,75	101,97	11,85	3,07	113,82	128,95
Daily standard deviation	5,19	4,66	61,23	30,41	3,88	0,08	36,41	42,65
Reversals (falling)	151,86	131,54	7208,80	6527,09	216,00	234,76	4316,50	2646,70
Reversals (rising)	185,14	103,48	8218,60	7659,74	320,00	353,55	4972,00	2266,98
Variability in daily flows	0,08	0,04	0,27	0,02	0,06	0,01	0,17	0,05
Mean daily flows	62,26	44,49	228,27	109,25	68,26	12,21	251,55	292,25
Median daily flows	52,87	47,71	226,48	117,39	53,84	8,64	243,07	306,65

Hydrological Variables	**SA**				**CVGD**			
	NF		**HP**		**NF**		**HP**	
	Mean	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**
Skewness daily flows	1,74	0,88	1,15	0,36	1,30	0,44	1,39	0,56
Ranges in daily flows (10/90)	0,91	0,04	0,65	0,21	0,91	0,03	0,74	0,06
Ranges in daily flows (25/75)	0,95	0,02	0,68	0,08	0,94	0,02	0,80	0,08
Spreads in daily flows (10/90)	0,06	0,07	0,01	0,01	0,02	0,00	0,05	0,04
Spreads in daily flows (25/75)	0,07	0,07	0,01	0,01	0,02	0,00	0,02	0,02
Annual maximum of 1 day means of daily discharge	324,70	208,90	859,78	402,60	344,60	191,77	1387,85	1517,67
Annual maximum of 3 day means of daily discharge	287,48	188,64	743,20	314,48	300,62	161,53	1295,83	1448,39
Annual maximum of 7 day means of daily discharge	242,74	166,27	634,49	257,91	252,53	123,78	1144,44	1301,86
Annual maximum of 30 day means of daily discharge	161,47	118,48	483,16	202,09	178,40	76,93	778,22	893,47
Annual maximum of 90 day means of daily discharge	130,76	99,33	394,59	171,63	136,09	62,96	575,96	673,22

Hydrological Variables	SA				CVGD			
	NF		HP		NF		HP	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Annual minima of 1 day means of daily discharge	15,45	13,41	44,50	26,41	8,59	8,07	62,45	79,97
Annual minima of 3 day means of daily discharge	15,55	13,49	48,36	28,65	8,74	8,17	64,04	81,97
Annual minima of 7 day means of daily discharge	15,78	13,65	53,49	32,08	9,04	8,17	66,67	85,31
Annual minima of 30 day means of daily discharge	16,92	14,52	65,59	39,87	10,19	7,98	72,61	92,48
Annual minima of 90 day means of daily discharge	18,75	16,66	82,69	46,38	13,62	6,03	81,60	102,38
Variability in annual maximum of 1 day means of daily discharge	0,60	0,15	0,75	0,14	0,64	0,01	1,33	0,94
Variability in annual maximum of 3 day means of daily discharge	0,58	0,13	0,65	0,12	0,60	0,02	0,41	0,26
Variability in annual maximum of 7 day means of daily discharge	0,60	0,17	0,58	0,11	0,57	0,02	0,44	0,22
Variability in annual maximum of 30 day means of daily discharge	0,73	0,28	0,52	0,13	0,55	0,02	0,51	0,24

Hydrological Variables	**SA**				**CVGD**			
	NF		**HP**		**NF**		**HP**	
	Mean	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**
Variability in annual maximum of 90 day means of daily discharge	0,78	0,52	0,50	0,17	0,49	0,02	0,57	0,28
Variability in annual minima of 1 day means of daily discharge	0,43	0,59	0,29	0,07	0,28	0,16	0,24	0,04
Variability in annual minima of 3 day means of daily discharge	0,44	0,56	0,26	0,03	0,27	0,16	9,63	13,25
Variability in annual minima of 7 day means of daily discharge	1,10	2,03	0,30	0,06	0,27	0,15	0,22	0,03
Variability in annual minima of 30 day means of daily discharge	0,61	0,81	0,36	0,16	0,27	0,11	0,24	0,03
Variability in annual minima of 90 day means of daily discharge	0,41	0,25	0,39	0,12	0,27	0,09	0,35	0,18

Appendix C.

Table C.1. Community parameters of the different ecological levels of organization by hydrogeomorphic zones. Richness (S), Abundance (N), Diversity (H’).

Ecological organization level	Community Parameters	Hydrogeomorphic zones							
		Sub-Andean				Central Valley Gravel Dominated			
		NF		HP		NF		HP	
		Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient
Overall invertebrates	S	64	0,28	40	0,33	37	0,29	34	0,41
	N	7432	0,58	1951	0,89	6281	0,83	2512	0,71
	H'	1,72	0,24	1,63	0,24	1,2	0,18	1,28	0,37
EPT	S	39	0,34	16	0,72	14	0,15	13	0,61

Ecological organization level	**Community Parameters**	**Hydrogeomorphic zones**							
		Sub-Andean				**Central Valley Gravel Dominated**			
		NF		**HP**		**NF**		**HP**	
		Value	**Variation Coefficient**	**Value**	**Variation Coefficient**	**Value**	**Variation Coefficient**	**Value**	**Variation Coefficient**
	N	3355	0,73	1256	1,5	3333	0,9	632	1,38
	H'	1,85	0,29	1,19	0,69	1,26	0,72	1,17	0,42
Predators	S	17	0,39	16	0,45	12	0,52	12	0,66
	N	373	0,65	93	0,64	360	1,13	105	0,93
	H'	0,94	2,38	0,74	1,72	0,28	1,03	0,53	1,01
Gatherers	S	23	0,36	13	0,48	12	0,2	11	0,43

Ecological organization level	Community Parameters	Hydrogeomorphic zones							
		Sub-Andean				Central Valley Gravel Dominated			
		NF		HP		NF		HP	
		Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient
	N	4686	0,59	1157	0,7	2336	0,83	1720	0,92
	H'	1,11	0,43	0,95	0,57	0,52	0,71	0,71	0,62
Shredders	S	12	0,62	3	0,85	2	1,24	2	1,56
	N	1215	1,66	116	1,22	8	1,73	34	2,17
	H'	0,26	1,29	0,03	2,32	0	0	0,04	0
Scrapers	S	7	1,31	4	0,99	5	1,08	5	0,6

Ecological organization level	Community Parameters	Hydrogeomorphic zones							
		Sub-Andean				Central Valley Gravel Dominated			
		NF		HP		NF		HP	
		Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient	Value	Variation Coefficient
	N	39	1,64	70	1,61	181	2,29	224	1,04
	H'	0,03	3,48	0,18	1,71	0,25	1,36	0,33	1,03
Filterers	S	2	0,31	2	0,93	3	0,42	1	1,03
	N	950	1,03	438	2,26	3171	0,99	389	1,87
	H'	0,08	2,62	0,02	3,77	0,05	1,41	0	0

Appendix D.

Table D.1. Differences in invertebrate assemblages (Bray–Curtis dissimilarity based on abundances) between flow regime categories (NF, HP), functional process zones (SA: Sub-Andean; CVGD, Central Valley Gravel Dominated) for the Biobío and Imperial rivers. PERMANOVA results are provided for all invertebrate, EPT groups and functional guilds. * p <0,05 ** p <0,001.

Ecological level	**Flow Regime Category**		**Functional Process Zone**	
	Pseudo-F	***P***	**Pseudo-F**	***P***
Overall invertebrates	6,394	0,001	12,156	0,001
EPT	6,565	0,001	13,007	0,001
Predators	3,771	0,001	9,552	0,001
Gatherers	2,885	0,012	15,744	0,001
Shredders	2,575	0,021	9,679	0,001
Scrapers	2,486	0,038	5,177	0,002
Filterers	4,072	0,015	4,698	0,015

8 CAPITULO III “COMPLEX INTERPLAY OF GEOMORPHOLOGY AND HYDROLOGY GOVERN FISH ASSEMBLAGES ACROSS A RIVER NETWORK INFLUENCED BY DIFFERENT WATER RESOURCE DEVELOPMENT LEVELS”

8.1 Introduction

The interplay of the flow regime with the physical template is important in determining the character of ecological communities in river ecosystems (cf. Walker et al., 1995, Poff et al, 1997; Ricther et al., 1997). This is primarily based on the work of Walker et al., (1995) who stated that the flow regime was the maestro that orchestrated the spatial and temporal character of ecological communities across a range of scales in river ecosystems. While Southwood (1977; 1988) stated that the physical character of rivers provides the template upon which all evolutionary process operates. The flow regime through the flow components such as magnitude, duration, timing and rate of change influences the physical habitat components (Poff et al., 1997; Belmar et al., 2013) such as the shape and size of river channels, wetted area (Rolls et al., 2012); bars, benches and islands (Ligon et al., 1995); pools and riffles (Erskine et al., 1999); organic matter (Gawne et al., 2000); and substrate composition (Sherrard & Erskine, 1991). In turn, the interaction of both act as filter of species, inducing an increase or decrease of some taxa and causing shifts according to functional traits (Poff et al., 2007; Carlisle et al., 2011), determining the distribution, diversity and abundances of biological communities in river systems (Schlosser 1982, Ward et al., 1999, Nilsson & Svedmark 2002). These community changes are driven by the control of life cycles of species that constitute them by controlling their spawning (Montgomery et al. 1983, Nesler et al., 1988; Copp 1989), recruitment (Almodovar & Nicola, 1999), feeding, mortality and growth rate (Lagarrigue et al., 2002).

To disentangle the role of hydrology, geomorphology and their interplay in shaping biological communities in river systems an interdisciplinary approach is required. Thoms & Parsons (2002) and Dollar et al. (2007) proposed a successful framework that facilitates the integration of disciplinary efforts in understanding and management of river systems. This framework integrates the geomorphology, hydrology and ecology and emphasizes that each of them must be organised hierarchically considering appropriate scales for the questions being set in studies of a river system. The transcendence of it lies in this integration and assessment of interplay that is essential for understanding the role of physical structure of a river system as the driver of ecosystem function and provision of services. This, in turn, will allow application of solutions to environmental problems in river systems and their effective management (Dollar et al., 2007; Vaughan et al., 2009; Gilvear et al., 2016). Limited number of studies, however, investigated directly this interplay and those available concentrated on single scale and/or incorrectly matched the scales among disciplines (cf de Fontaine and Rogers, 1999; Parsons & Thoms, 2003 and 2007, Webb et al., 2011; Gurnell et al., 2012). As a consequence, possible failure to place a problem at the correct scale may result in incorrect interpretations of pattern and process and can cause misguided management efforts.

Recently proposed Riverine Ecosystem Synthesis (RES) offers a framework that can be used for integration of geomorphology, hydrology and biota across temporal and spatial scales (Thorp et al., 2008). The RES, describes rivers as arrays of large hydrogeomorphic zones, called Functional Process Zones (FPZs), formed by factors such as regional geology, valley conditions, geomorphic structure of the channel and valley, climate, and hydrologic patterns (cf., Montgomery 1999; Poole 2002; Thoms and Parsons, 2002; Thorp et al. 2006, 2008). These FPZs occur repeatedly longitudinally along river systems have the adequate spatial size to capture hydrogeomorphic variations and serve as a template for biological functional zones (Thorp et al., 2008; McCluney et al 2014; Thoms et al., 2018).

Chilean rivers are under intense water resource development pressure. For example, a construction of 210 new hydropower projects larger than 20 MW, and 447 smaller projects planned up to 2050 (Chilean Ministry of Energy, 2016; Díaz et al., 2019). Previous studies by Habit et al. (2007) reported changes in fish assemblages and populations in Chilean river systems that were subjected to flow regulation. Specifically, they showed that flow alteration by hydropower caused the decrease in fish abundances and the effect was the strongest for species that inhabited the water column (Habit et al., 2007). Furthermore, hydropower flow alterations have also been shown to modify fish habitat suitability by influencing quantity, quality and location of different habitats (Garcia et al., 2011). These studies, however, did not disentangle the specific role or complex nature of interplay between hydrology and geomorphology in shaping fish assemblages across spatial and temporal scales. Disentangling this interplay is expected to have broad implications as it would allow understanding of cause - effect mechanisms in river systems and, therefore, would allow predicting their future states. This, in turn, can be instrumental for sustainable water resource management to benefit the in-stream and floodplain ecology as well providing healthy riverine habitats and sufficient water supply for the society.

The aim of this study was to assess the interplay of flow regime and geomorphology as drivers of fish assemblages across a range of scales in an Andean River system subjected to intense flow manipulations. To do this, we first established the Functional Process Zones (FPZs) in two river basins in Central Chile with and without flow alteration due to hydropower development. Secondly, we identify different flow management categories within FPZs using hydrological indexes. Thirdly, we stablished a hydrogeomorphic zones as FPZs characterised by different flow management. Finally, we compared taxonomic and functional fish assemblage structure among FPZs, flow management categories and hydrogeomorphic zones.

8.2 Methods.

8.2.1 Study Area

The study was conducted in the Biobío and Imperial River basins in central Chile (Figure 8.1). These basins are located between 36° and 39° Lat. S (Biobío) and 37° and 38° Lat. S (Imperial) and have catchment areas of 24,260 km^2 and 12,763 km^2, respectively. There are three main physiographic regions within these two basins that vary in elevations, geology and climate. The Andes Ranges, the most easterly region, with elevations extending from 1700 to above 2500 m ASL are dominated by various forms of volcanic rocks and are the main runoff and sediment source areas for both the Biobío and Imperial rivers. The Central Valley is a large depositional region of lower elevations and slopes between the Andes and Coastal Ranges. Here, the surficial geology is dominated by an array of aeolian, colluvial and alluvial deposits of sands and gravels. The Coastal Range is a complex region of intertwined metamorphic and granite rocks and landforms that have elevations between 650 and 1000 m ASL. The Biobío and Imperial Rivers that drain these physiographic regions are typical Andean river systems with headwaters in the Andes that flow directly to the coast (Marin et al., 2006). Thus, they are relatively short, straight, high energy river systems; the length of the main river channels of the Biobío River is 407 km while the Imperial River is 237 km. Overall, the Biobío and Imperial rivers experience a wet temperate climate with a Mediterranean influence resulting in average annual rainfalls of 1200 to 4000 mm. Annual rainfall varies across both basins, with maximum rainfall in the Andes, lowest in the Central Valley and slightly higher in the Coastal Ranges. Both basins are characterised by pluvio-nival hydrological regime. The upper reaches closer to the Andes are characterised by higher mean monthly discharges between July and December as a result of rainfall and seasonal snow melt, while the pluvial regime of the central valley supplies additional high discharges due to higher rainfall in June and July. Long term daily discharges for the Biobío and Imperial rivers at the mouth are 899 and 240 m^3s^{-1}, respectively.

There are seven distinct Functional Process Zones (FPZs) – large stretches of river within the river network with similar geomorphic features – in the Biobío and Imperial Rivers (Figure 8.1). These, FPZs are delineated and named based on statistically derived features from the river network of the river channel and surrounding valley along with geological and precipitation information (Elgueta et al., 2019, see Chapter I). The character of the functional process zones for the Biobío and Imperial rivers are provided in Table 8.2. Four Functional Process Zones are common to both basins (Sub-Andean, Central Valley Gravel Dominated, Central Valley Cobble Dominated and Lowland), two are exclusive to the Biobío basin (Andean and Reservoir) and one (Tortuous alluvial) is only found in the Imperial basin (Figure 8.1 and Table 8.1). Sub-Andean FPZ is generally located at 730 m ASL and is characterised by high energy slopes and semi-confined valleys. Central Valley Gravel Dominated FPZ is located at an average elevation of 94 m ASL and has large valley widths (up to 4432 m) and has lower down valley slopes (DVS: 0.003). In contrast Lowland FPZ is located in the lower altitudes, below 37m ASL and here the river channel is contained in wide valleys (VW: 13245 and VTR: 7552) with low down valley slope (DVS: 0.002).

Table 8.1. Character of functional process zones in Biobío and Imperial river basins.

Functional Process Zones	**Character**
Andean (An)	This FPZ is found at an average elevation of 1132 masl, with an average annual rainfall of 1629 mm. It flows in a compressed and highly confined channel with high lateral slopes (RVS: 0.39 and LVS: 0.36) and low sinuosity of 1.1. This FPZ is found only in the Biobío basin, and covers a length of only 15 km.
Sub-Andean (SA)	Located at an average elevation of 730 masl, has a mean annual rainfall of 1857 mm, and valleys that are semi-confined and sinuous, with steep longitudinal slopes. As for its spatial distribution, of the total 440 km of length of this FPZ, 290 km are in the Biobío basin and 150 km in the Imperial. The riverbed is composed mainly of sediments with grain size larger than 600 mm in diameter (large boulders), with patches of smaller boulders (300-600 mm).
Reservoir (Re)	Found only in the Biobío basin, to elevation of 387 and covers a length of 55 km. It is characterized by the presence of large hydroelectric dams. It has confined valleys with high lateral slopes.

Functional Process Zones	Character
Central Valley Cobble Dominated (CVCD)	Located at an average altitude of 289 masl and has a wide valley of 3158 m with low lateral slopes (Right valley slope: 0.063, Left valley slope: 0.077) and unconfined valleys with low longitudinal slopes (Down valley slope: 0.007). Its geology is characterised by fluvial deposits, with sediments that have accumulated over a long time such as pebbles and gravel on top of finer sediments, such as sand. Of the 385 km covered by this FPZ, 120 km are in the Biobío basin and 265 km are in the Imperial basin.
Central Valley Gravel Dominated (CVCD)	Located at an average elevation of 94 masl, with a mean annual rainfall of 1262 mm, this FPZ has a mean valley width of 4432 m and low longitudinal slope (Down valley slope: 0.003). Its geology is characterised by sedimentary fluvial deposit sections, with stretches of alluvial deposits made up of rocks, gravel, sand, and silt. It covers 690 km of total river length that was analysed, of which 255 km are in the Biobío basin and 435 km are in the Imperial basin.
Tortuous Alluvial (To)	This FPZ with length of only 15 km is found only in the Imperial basin. It is characterised by a single channel with high sinuosity. It also has wide valleys, low lateral slopes, and low longitudinal gradients (Right valley slope: 0.056 y Left valley slope: 0.046).
Lowland (Lo)	This FPZ has a low average altitude of 37 masl, and mean annual precipitation of 1186 mm. It has straight channels and wide valleys with low lateral slopes, low longitudinal valley slopes and very low sinuosity. Is characterized by fine sediments and sands, muddy areas are also observed. It covers 145 km, of which 75 km are in the Biobío basin and 70 km are in the Imperial basin.

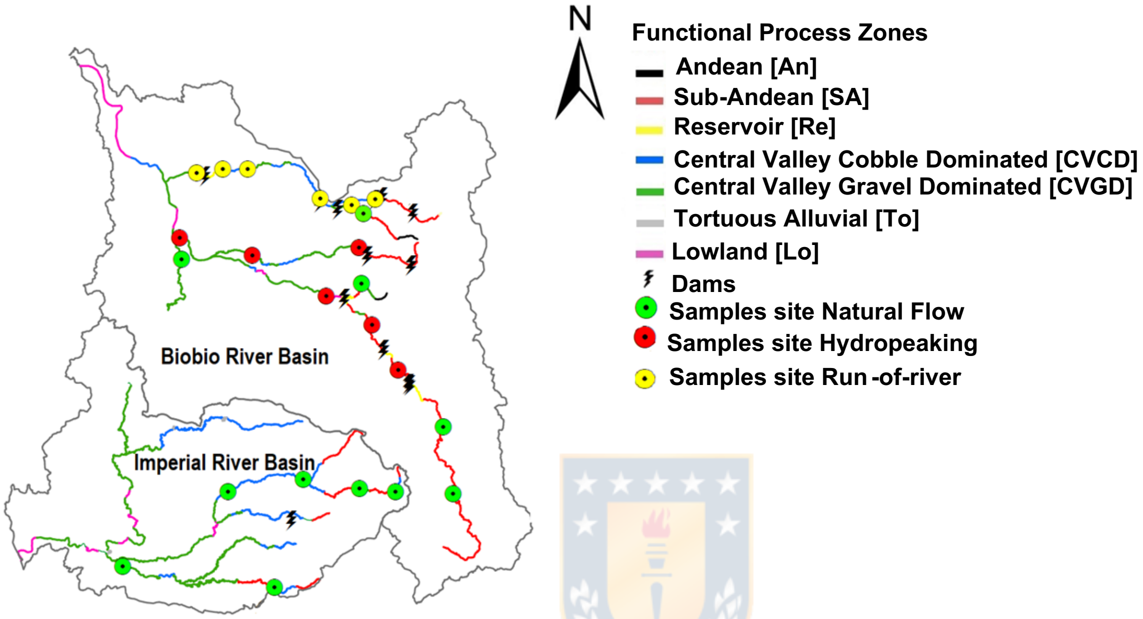

Figure 8.1. Biobío and Imperial river basins showing the FPZs and dam locations within each network. Circles represent fish sampling sites in FPZs subjected to different flow management categories. Detailed description of FPZs are provided in table 1.

Land use characteristics vary across both river basins. Native forest and forestry plantations are the dominant land cover of the Andes and Coastal Ranges, while agricultural activities are more prominent in the Central Valley. Since the 1970s flow management through the construction of dams and weirs have occurred, principally for electricity generation. There are 11 hydroelectric power plants regulating flows along the Biobío River and its major tributaries (Laja and Duqueco Rivers). Three hydropeaking dams with large reservoirs that are characterised by hourly generation are located in the Biobío River basin. From upstream to downstream: Ralco (height (H) = 155 m; total volume (TV) = 1222 mm^3; operating since 2004), Pangue (H=113 m; TV = 175 mm^3; operating since 1998) and Angostura (H=50 m; TV = 100 km^3; since 2013). Furthermore, there are two smaller hydropeaking dams (H=15 m each, since 2007) without reservoir in the Biobío river basin located on Duqueco river tributary (TV = 1900 km^3; operating since 2016). The remaining hydroelectric dams in the Biobío basin operate as run-of-river (Valdovinos & Parra, 2006; García, et al., 2011). Furthermore, there is one run-of-river dam in the upper Imperial Basin, located in the Trueno River tributary (Figure 8.1). This small Trueno dam in Imperial River was not considered in analyses presented here. There have been no detailed hydrological analyses of the impact of these dams on the long or short-term flow regime of the rivers. García et al., (2011), however, suggested that marked increases in daily and sub-daily flow fluctuations.

Fish fauna of both rivers have been previously characterised, and fish communities are similar between the two rivers (Ruiz,1993, Habit et al., 2005, Garcia et al., 2011; and Vila & Habit, 2015). The fish community of the Biobío river basin is composed by 18 native species and 5 non-native species, while there are 15 native and 5 non-native fish species recorded for the Imperial River basin (Vila & Habit, 2015; Table 8.2). These fish assemblages are characterized by longitudinal zonation based on nested subsets. Thus, zonation does not result from species replacement along the river, but rather from an accumulation of species from up to downstream (Habit et al., 2007b). Therfore, potamal zones hold more diverse and abundant fish assemblage (Habit et al., 2007b). Habitat preference of the different species has been previously described and classified into two broad categories based on their position in the water column (García et al., 2011). Benthic species inhabit directly above or within the bottom substrate, whereas open water species actively swim using any depth of the water column (García et al., 2011, Table 8.2).

Table 8.2. Fish species recorded in the Biobío and Imperial river basins. Functional guilds are based on habitat preferences in benthic and open water species. * Indicate species that were collected in this study.

Fish groups	**Species**	**Acronym**	**Biobío River**	**Imperial River**	**Benthic**	**Open water**
Native	*Aplochiton zebra*	*At*	X			X
	Basilichthys microlepidotus	*Bmi*	X*	X*		X
	Brachygalaxias bullocki	*Bb*	X	X		X
	Bullockia maldonadoi	*Bm*	X*	X*	X	
	Cheirodon galusdae	*Chg*	X*	X*		X
	Diplomystes nahuelbutaensis	*Dn*	X*	X	X	
	Geotria australis	*Ga*	X*	X*	X	
	Galaxias maculatus	*Gm*	X*	X*		X
	Mordacia lapicida	*Ml*	X	X	X	
	Nematogenys inermis	*Ni*	X	X*	X	
	Odontesthes mauleanum	*Omau*	X*	X		X
	Odontesthes brevianalis	*Ob*	X	X		X
	Percillia irwini	*Pi*	X*			X
	Percillia gillissi	*Pg*		X*		X
	Percichthys trucha	*Pt*	X*	X*		X
	Percichthys melanops	*Pm*	X	X		X
	Trichomycterus areolatus	*Ta*	X*	X*	X	
	Trichomycterus chiltoni	*Tch*	X		X	
Non-native	*Cyprinus carpio*	*Cc*	X*	X		X
	Carassius carassius	*Cca*	X*	X		X
	Gambusia holbrooki	*Gh*	X*	X		X

Fish groups	Species	Acronym	Biobío River	Imperial River	Benthic	Open water
	Oncorhynchus mykiss	*Om*	X*	X*		X
	Salmo trutta	*St*	X*	X*		X

8.2.2 Hierarchical organisation of this study

Three domains were recognised for the purpose of this study: hydrology, geomorphology and ecology. Each of the domains is hierarchically organised. Flow magnitude, frequency, duration, seasonality and variation were used to characterise the hydrology domain at three temporal scales: long term, daily and sub-daily. Geomorphology of the Biobío and Imperial rivers was characterised by a set of 16 variables at three different spatial scales: catchment, valley and river channel. Finally, ecology domain considered fish assemblage structure and was assessed at three levels of organization: assemblages (all fish), native and non-native fish, and individual habitat preference (benthic and open water).

8.2.3 Flow regime

Daily and sub-daily flow data were available for 15 gauging stations throughout the Biobío and Imperial rivers (N=30 years; see Chapter II). These data were accessed from the National Water Division of Chile (DGA). For each data set, 41 hydrological variables (Table 8.3) representing the magnitude, frequency, duration, seasonality and variability of the flow regime were calculated (cf. Richter et al., 1997 & 1998; Thoms and Parsons, 2003). This was done for three different time periods or scales: long term (annual), daily and sub-daily (Table 8.3). These hydrological variables were then grouped into three flow categories, based on the type of flow management dominating the flow regime. The first category was natural flow (NF) located in river zones not influenced by upstream dams. Run-of-river (ROR) was the second group, corresponding to flow regime in river zones influenced by small upstream dams. The third flow group was the hydropeaking group (HP), which occurred in river zones located downstream of large dams whose operations are designed to meet sub-daily power generation demands. Statistical differences in the flow character of the three flow groups – NF, ROR and HP – were assessed by Analysis of Similarity (ANOSIM), and those hydrological variables contributing to the within flow group similarity were determined using a Similarity Percentages Analysis (SIMPER) (cf. Thoms and Parsons, 2003), see Chapter II.

Table 8.3. Hydrological variables used to investigate the flow regime of the Biobío and Imperial river basins. Time scale analysis: Sub-daily (SD), daily (D), long time (LT).

Hydrologic index	**Time scale**	**Description**
Sub-daily flow fluctuations	SD	Difference between the maximum and the minimum daily discharge. This value is normalized by the mean daily discharge to account for differences in river and catchment scales.
Flow-ramping rate	SD	Change in discharge between two successive discharge observations divided by the observation time interval.
Coefficient of variation of rise rate	SD	Rise rate divided by median daily flow.
Rise rate	SD	Average rate of positive changes in flow from one day to the next divided by median daily flow.
Fall rate	SD	Average rate of negative changes in flow from one day to the next divided by median daily flow.
Coefficient of variation of fall and rising rate	SD	Fall rate or rise rate divided by median daily flow.
Daily minimum	D	Lowest measured flow during a 24-h period (Qmin).
Daily maximum	D	Highest measured flow during a 24-h period (Qmax).
Daily delta	D	Difference between daily minimum and daily maximum represents the amount of daily flow change.
Daily standard deviation	D	The common statistical calculation of the 24-hourly flow values.

Hydrologic index	Time scale	Description
Reversals (falling and rising)	D	Number of changes between rising and falling periods of the hydrograph; adapted from a similar metric derived with daily data (Richter et al., 1996; TNC, 2007).
Variability in daily flows	D	Daily flow averages for each year and then averaged across years.
Mean daily flows	LT	Mean daily flow.
Median daily flows	LT	Median daily flow.
Skewness in daily flows	LT	Mean daily flows divided by median daily flows.
Ranges in daily flows (10/90th), (25/75th)	LT	Ratio of 10th/90th and 25th/75th percentiles in daily flows overall years.
Spreads in daily flows (10/90th), (25/75th)	LT	Ranges in daily flows divided by median daily flows.
Annual minima or maximum of 1-/3-/7-/30-/90-day means of daily discharge	LT	Magnitude of minimum or maximum annual flow of various duration, ranging from daily to seasonal (Low and high flow)
Variability in annual minima or maximum of one-/3-/7-/30 /90-day means of daily discharge	LT	Coefficient of variation of annual minima or maximum of 1-/3-/7-/30-/90-day divided by means of daily discharge (Low and high flow).

8.2.4 Geomorphology

For geomorphology characterisation, data collected by Elgueta et al., 2019 (see Chapter I) were used. Thus, FPZs were determined for both studied basins using 16 geomorphic variables: 3 at the catchment scale, 7 at the valley scale and 6 at the channel scale. The 16 variables were determined in 160 (Imperial River basin) and 187 (Biobío River basin) sites, corresponding to 5 km intervals using a series ArcGIS functions and tools (Harris et al., 2008 and Bradley et al., 2016). Subsequently, the dataset was analysed using a variety of multivariate statistical techniques that identified groups of sites with a similar geomorphology. The data were classified using the flexible unweighted pair-group method with arithmetic averages (UPGMA) fusion strategy, as recommended by Belbin & McDonald (1993). Once identified, these similar groups were then arrayed onto the streamlines of the Biobío and Imperial Rivers, to delineate the position of sites with similar morphological character (using standard GIS mapping techniques).

8.2.5 Fish sampling

Fish sampling was undertaken at a total of 23 sites in the Biobío and Imperial river basins. Sites were selected in both basins to represent different flow categories (NF, ROR and HP) and FPZs shared between the two river basins (SA: Sub-Andean, CVCD: Central Valley Cobble Dominated, CVGD: Central Valley Gravel Dominated). This was done in order to disentangle the effect of the various flow regimes and geomorphological characteristics of the channel within the river network. Access to some sites was inaccesible, and as a result six different functional process zone - flow combinations - hydrogeomorphic zones – were sampled. These were SA-NF (7 sites); CVGD-NF (2 sites); CVCD-NF (2 sites); CVCD-ROR (6 sites); SA-HP (3 sites); and CVGD-HP (2 sites). Sampling sites in the regulated sections of the river network were located between 7 km and 50 km downstream of the dams.

At each site, fish sampling was undertaken using a standardized electrofishing technique. All habitats were proportionally sampled at each site with the total shocking time of 60 mins per site. Fishes were identified to species level, and also classified as native, non-native and into habitat preference guilds based on Ruiz (1993), Habit et al. (2005), Garcia et al. (2011) and Vila & Habit (2015).

The fish assemblage of the Biobío and Imperial Rivers was initially assessed using abundance, species richness and evenness as well as the Shannon's diversity index (H') for each site, and then aggregated for each flow group, functional process zone and then hydrogeomorphic zone (flow group * functional process zone). This was completed for goups of all fish, native species, non-native species and guilds based on habitat preference. Abundance of each group was the total number of individuals recorded at each site. These data were further analysed using a range of univariate and multivariate statistical techniques. Initially a one-way Analysis of Variance

(ANOVA) was used to determine if significant differences existed in species diversity (H`) among flow groups, functional process zones and hydrogeomorphic zones. The relative influence of abundance, richness and evenness on fish diversity was then investigated through the use of standard ternary diagrams which array the combined influence of each in three-dimensional space. This approach can highlight the influence of one or more variables and is a standard method in geomorphology but is infrequently used in river science (cf. Thoms et al., 2018). In addition, further statistical analyses of fish species abundance in the various flow groups, functional process zones, and hydrogeomorphic zones were undertaken via an ANOSIM (Clarke et al., 2006). ANOSIM allows a permutation-based hypothesis testing and tests for differences among groups of samples from different groups (significance level $p < 0.05$) and the degree of similarity: R=1 means high dissimilarity and R=0 means low dissimilarity or high similarity (Carreón-Palau et al., 2017). R values < 0.3 suggest no differentiation among groups, those >0.30 and <0.70 overlap but are different, and R value >0.70 suggest significant difference among groups (Warwick and Clarke, 1993). The contribution of each species to the mean dissimilarity in fish assemblage structure for different groups (i.e., flow group, functional process zone and hydrogeomorphic zone) was then undertaken with a SIMPER analysis. SIMPER identifies those species primarily responsible for discriminating between two observed sample clusters (Clarke and Warwick, 2001). For this analysis, species providing ≥ 5% contribution to discrimination within a single period were used. Finally, the variance of abundance for each group was determined according to the rank dissimilarity used to compute the comparative Index of Multivariate Dispersion (IMD; Warwick and Clarke 1993). The multivariate measure of rank dissimilarity (MVDISP; Clarke and Warwick 2001) was used in this study to determine if the variance of abundance for the three groups differed. Others have used this metric to indicate level of disturbances (Habit et al., 2007a).

8.2.6 Environmental drivers on fish assemblages

Distance-based linear modelling (DISTLM) was used to assess the principal geomorphological and hydrological variables driving different fish responses.

DISTLM is a multiple multivariate regression analysis that uses permutation to test for the strength and significance of relationships between predictor (i.e. hydrological and geomorphological variables at different spatial and temporal scales) and ecological variables (i.e. assemblage structure at a given ecological organisation level). Subsequently, proportion of significant variables with a proportion of explained variation above 90th percentile based on marginal tests was calculated for each domain and scale category (catchment, valley, river channel for geomorphologic variables and long-term, daily and sub-daily for hydrological variables).

8.3 Results

8.3.1 Flow regime

Based on hydrological indicators, significant differences were observed among the three flow groups: natural flow, run-of-river and hydropeaking (ANOSIM, Global R: 0.401, $P = 0.001$). Pairwise comparisons revealed significant differences between natural flow and run-of-river (R: 0.296, $P = 0.04$), natural flow and hydropeaking (R: 0.584, $P = 0.001$) as well as between run-of-river and hydropeaking (R: 0.299, $P = 0.012$). Thus, three distinct flow groups are observed in the Biobío River basin and two are an artefact of human flow regulation. The flow regime character differs among the three flow groups and this difference can be attributed to the time scale of hydrological variables that characterised each of the flow regime groups. The main hydrological characteristics of natural flow regime (NF) correspond to slight or no change in the magnitude and frequency (rate of change) of flow at sub-daily and daily scales, with a mean difference in flow of 11 m^3/s in 24 hrs, that implies low sub-daily and daily flow variability. Run-of-river (ROR) is characterised by increases of magnitude and frequency of flow at sub-daily and daily scales, with change of 26 m^3/s in a 24 hrs that compared to NF implies slight increase of flow variability. Furthermore, the minimum flow on daily scale is lower in ROR compared to NF. Finally, hydropeaking (HP) strongly alters the magnitude, frequency and duration of flow at sub-daily, daily, and monthly time scales. As such, HP causes high sub-daily variation of flow with mean difference of 156 m^3/s in 24 hrs compared to NF.

8.3.2 Fish assemblages.

Fish diversity (Shannon-Wiener index) ranged between 0.28 and 1.76 and no significant differences were recorded among the three flow groups (ANOVA F (2,21): 0.84, *P* = 0.44). Furthermore, no significant differences in diversity were found among FPZs (ANOVA F (2,21): 0.84, *P* = 0.44) and hydrogeomorphic zones (ANOVA F(5,18): 0,57, *P* = 0.72).

Unpacking diversity into individual components of abundance, richness and evenness showed that overall, abundance varied among flow groups, FPZs and hydrogeomorphic zones (Figure 8.2). Fish abundance of native fish and fish that used open water habitats markedly decreased in Sub-Andean FPZ with a flow regime disturbed by hydropeaking. Thus, differences in fish assemblage structure appeared to be driven by differences in abundance (Figure 8.2).

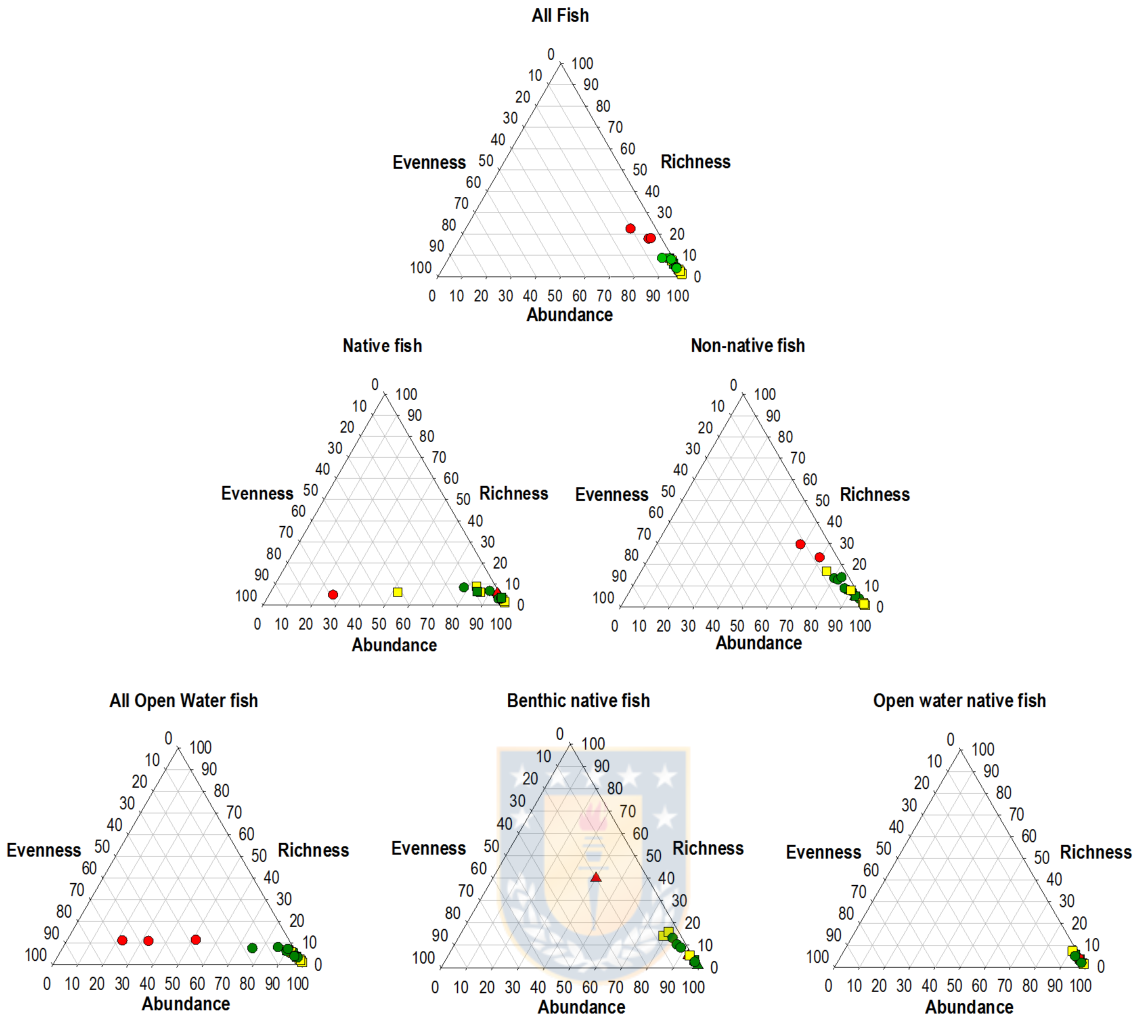

Figure 8.2. Abundance, richness and evenness relationships for different levels of ecological organization of the fish assemblage in the Biobío and Imperial rivers. FPZs are represented by circles (Sub-Andean), triangles (Central Valley Gravel Dominated) and squares (Central Valley Cobble Dominated). Colours represent flow groups: green (natural flow regime), yellow (run-of-river), red (hydropeaking).

There were no significant differences in fish abundance among flow groups, but differences among FPZs and hydrogeomorphic zones were significant (Table 8.4). Specifically, non-native fish and all fish that inhabit open water habitats showed significant differences in abundance between Sub-Andean FPZ and Central Valley Gravel Dominated FPZ, where non-native fish were more abundant in Sub-Andean

FPZs and native open water fish were more abundant in Central Valley Gravel Dominated FPZ. Furthermore, fish assemblages showed significant differences in abundance between reaches with natural flow and hydropeaking in both Sub-Andean and Central Valley Gravel Dominated FPZs. Non-native fish and open water fish showed significantly higher abundances in reaches with natural flow compared to reaches with hydropeaking in the Sub-Andean FPZ. Furthermore, native open water and benthic fish were characterised by significantly higher abundances in reaches with natural flow compared to reaches with hydropeaking in Central Valley Gravel Dominated FPZ. This suggests combined effect of flow and FPZs on fish abundance. Furthermore, this interplay is of complex nature and moderated by habitat occupied by fish.

The differences in the structure of species assemblage among flow groups, FPZs and hydrogeomorphic zones were clear at most of the ecological and spatial levels of organisation (Figure 8.3). When all fish species were considered *Percilia sp*., *Trichomycterus areolatus* and non-native *Oncorhynchus mykiss* strongly contributed to a higher similarity among flow groups, FPZs and hydrogeomorphic zones, meanwhile contribution of other species to similarty varied among groups and zones. For instance, in reaches with natural flow regime in Sub-Andean FPZ *Percilia sp.* and *O. mykiss* were the most abundant species, whereas in Central Valley Gravel Dominated FPZ with natural flow, *Percilia sp*. and *T. areolatus* dominated (Figure 8.3). Meanwhile, Sub-Andean FPZ was only dominated by *O. mykiss*, whereas in Central Valley Gravel Dominated FPZ only *Percilia sp*. Dominated in river reaches with hydropeaking. These changes were also evident at other levels of the ecological organisation of fish assemblage structure. For instance, the contribution of *Percilia* sp. increased within the native fish ecological level in hydrogeomorphic zones with hydropeaking, whereas other native species such as *Diplomystes nahuelbutaensis* and *Geotria australis* were absent. Among non-native species, the contribution of *Salmo trutta* was lower in reaches characterised by hydropeaking, whereas *Gambusia hoolbroki* was abundant in reaches with run-of-river flow regime in the CVCD FPZ.

Fish ecological organisation level based on habitat preferences also revealed significant differences among hydrogeomorphic zones (Figure 8.3). *Trichomycterus areolatus* had the highest contribution in most of the assemblages of benthic native species. Only in reaches with natural flow regime *D. nahuelbutaensis* also contributed to the assemblage similarity within Sub-Adean FPZ, and *B. maldonadoi* to the Central Valley Gravel Dominated FPZ. For native open water species, *Percilia sp*. had the highest contribution in most of the hydrogeomorphic zones. Three additional species (*Galaxias maculatus, Percichthys trucha* and *Basilichthys microlepidotus*) contributed significantly to this ecological level in Central Valley Gravel Dominated FPZ with natural flow regime. Their contribution, however, became insignificant in Central Valley Gravel Dominated FPZ with hydropeaking.

Table 8.4. Differences in fish assemblages between flow groups, functional process zones and hydrogeomorphic zones (flow groups by functional process zones) in the Biobío and Imperial Rivers. ANOSIM results are provided for all fish (White), Benthic fish (Gray) and open water (Dark gray), where non significant values (ns) were R <0.3, and significant values were considered between range of R = 0.3-0.7 (*) and R > 0.7 (**). Hydrogeomorphic zones are represented by numbers, where, 1: SA-NF, 2: SA-HP, 3: CVGD-NF, 4: CVGD-HP, 5: CVCD-NF, 6: CVCD-ROR.

Flow groups

Flow groups	All fish			native			Non native		
	NF	ROR	HP	NF	ROR	HP	NF	RO R	HP
NF									
ROR	ns ns ns			ns ns ns			ns ns ns		
HP	ns ns ns	ns ns ns		ns ns ns	ns ns ns		ns ns ns	ns ns ns	

Functional process zone

Functional process zones	All fish			Native			Non native		
	SA	CVGD	CVCD	SA	CVGD	CVCD	SA	CVGD	CVCD
SA									
CV GD	* ns *			ns ns ns			* - *		
CV CD	ns ns ns	ns ns ns		ns ns ns	ns ns ns		ns - ns	ns - ns	

Hydrogeomorphic zones

Hydrogeomorphic zones	All fish					
	1	2	3	4	5	6
1						
2	ns ns *					
3	* * **	* ns *				
4	* ns *	ns ns ns	ns ns ns			
5	ns ns ns	ns ns ns	ns ns ns	ns ns ns		
6	ns ns *	ns ns ns	ns ns ns	ns ns ns	ns ns ns	

	Native					
	1	2	3	4	5	6
1						
2	ns ns ns					
3	** * ns	ns ns ns				
4	ns ns ns	ns * ns	ns * *			
5	ns * ns	ns ns ns	ns ns ns	ns ns ns		
6	ns ns ns	ns ns ns	ns * ns	ns ns ns	ns * ns	

	Non-native					
	1	2	3	4	5	6
1						
2	* - *					
3	** - **	* - *				
4	** - **	ns - ns	ns - ns			
5	* - *	ns - ns	ns - ns	ns - ns		
6	* - *	ns - ns	* - *	* - *	* - *	

The index of multivariate dispersion of the fish assemblage structure (proxy of assemblage variability) differed among flow groups, FPZs and hydrogeomorphic zones at all ecological levels of organization (Figure 8.4). As such assemblage variability in natural flow group was lower compared to other flow groups at all ecological levels of organization, with the exception of benthic native fish. Conversely, the hydropeaking flow group was characterised by the highest multivariate dispersion when compared to other flow groups at all ecological levels of organization.

When functional process zones and all fish were considered, Sub-Andean FPZ and Central Valley Gravel Dominated FPZ had similar multivariate dispersion that was significantly lower compared to the multivariate dispersion recorded in the Central Valley Cobble Dominated FPZ. When only native fish were considered, Sub-Andean FPZ was characterised by the highest multivariate dispersion compared to Central Valley gravel Dominated and Central Valley Cobble Dominated FPZs, whereas Central Valley Gravel Dominated FPZ was characterised by the highest multivariate dispersion among all FPZs when only non-native fish were considered (Figure 8.4).

Multivariate dispersions of fish assemblages in FPZs in reaches with altered flow regime (both hydropeaking and run-of-river) were higher compared to their analogous FPZs in reaches with natural flow regime when all fish and native fish were considered (Figure 8.4). Likewise, non-native fish in Sub-Andean FPZ showed higher multivariate dispersion when under influence of hydropeaking compared to natural flow regime. When habitat preferences were considered, native benthic fish in both Sub-Andean FPZ and Central Valley Gravel Dominated FPZ with hydropeaking showed higher dispersion than analogous FPZs with natural flow regime. Conversely, Central Valley Cobble Dominated FPZ with natural flow was characterised by higher multivariate dispersion than Central Valley Cobble Dominated FPZ with run-of-river regime (Figure 8.4). Furthermore, all open water fish habitat and native open water fish in Sub-Andean FPZ and Central Valley Cobble Dominated FPZ with altered flow regimes were characterised by higher dispersion than the analogous FPZs in reaches with natural flow regime. The multivariate dispersion range also differed among flow groups and FPZs, where the values fluctuate between 0.69 and 1.29 for the flow groups and between 0.50 and 1.57 for the FPZs

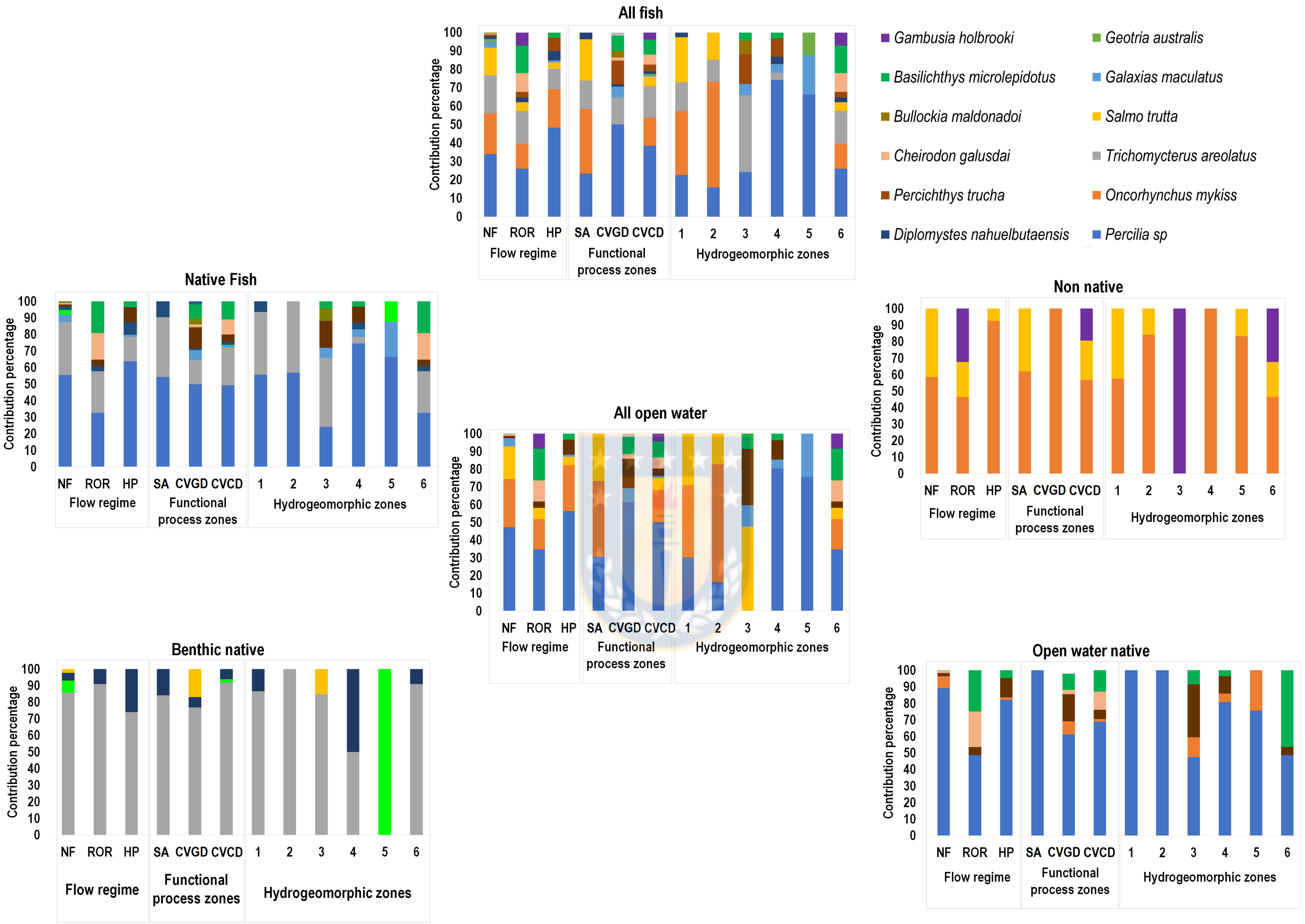

Figure 8.3. Simper analysis of fish assemblages at different ecological levels of organization in the Biobío and Imperial rivers

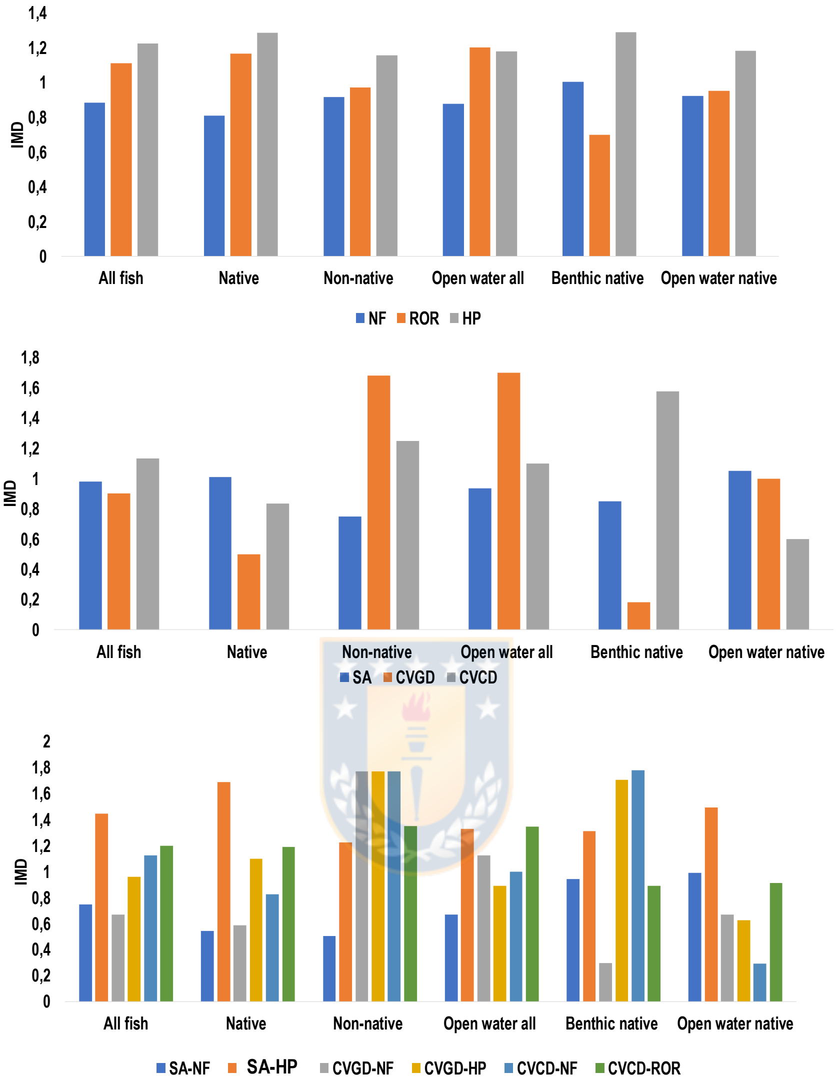

Figure 8.4. The index of multivariate dispersion of fish species abundance at different ecological levels of organization for the various flow groups (A), functional process zones (B) and hydrogeomorphic zones (flow group by functional process zones; C) in the Biobío river. Variance was determined via the multivariate dispersion index (IMD).

8.3.3 Environmental drivers

Both, hydrology and geomorphology had an influence on fish assemblage at all ecological levels, but this influence differed among FPZs and ecological levels of organisation (Figure 8.5). In Central Valley Gravel Dominated FPZ, hydrology and geormorphology variables had a strong representation as driver of responses of fish at all ecological levels. Different scenario was observed for the Sub-Andean and Central Valley Cobble FPZs in which the level of influence of dominated the influence of hydrology and geormorphology variables varied in the ecological levels. Fish assemblage that considered all fish species was strongly driven by both hydrology and geomorphology variables and across all spatial and temporal scales in all FPZs (Figure 8.5). At lower levels of ecological organisation, benthic and open water native fish were influenced by long-term hidrological variables in the three FPZs but the influence of daily and sub-daily variables was more important in valley zones. This efect was slightly stronger for open water fish. As such, non-native fish assemblage responded to daily and sub-daily flow variables in all FPZs but to long-term variables only in the CVGD FPZ. Furthermore, non-native fish assemblages were driven by geomorphic variables at valley scale in all FPZs, whereas variables at catchment and channel scale were of influence on non-native fish only in the SA FPZ and CVGD FPZ but not CVCD FPZ. Finally, daily and subdaily flow variables had a strong influence on fish responses in FPZs located in the Central Valley independently of flow regime categories (Hydropeaking or Run-of-River)

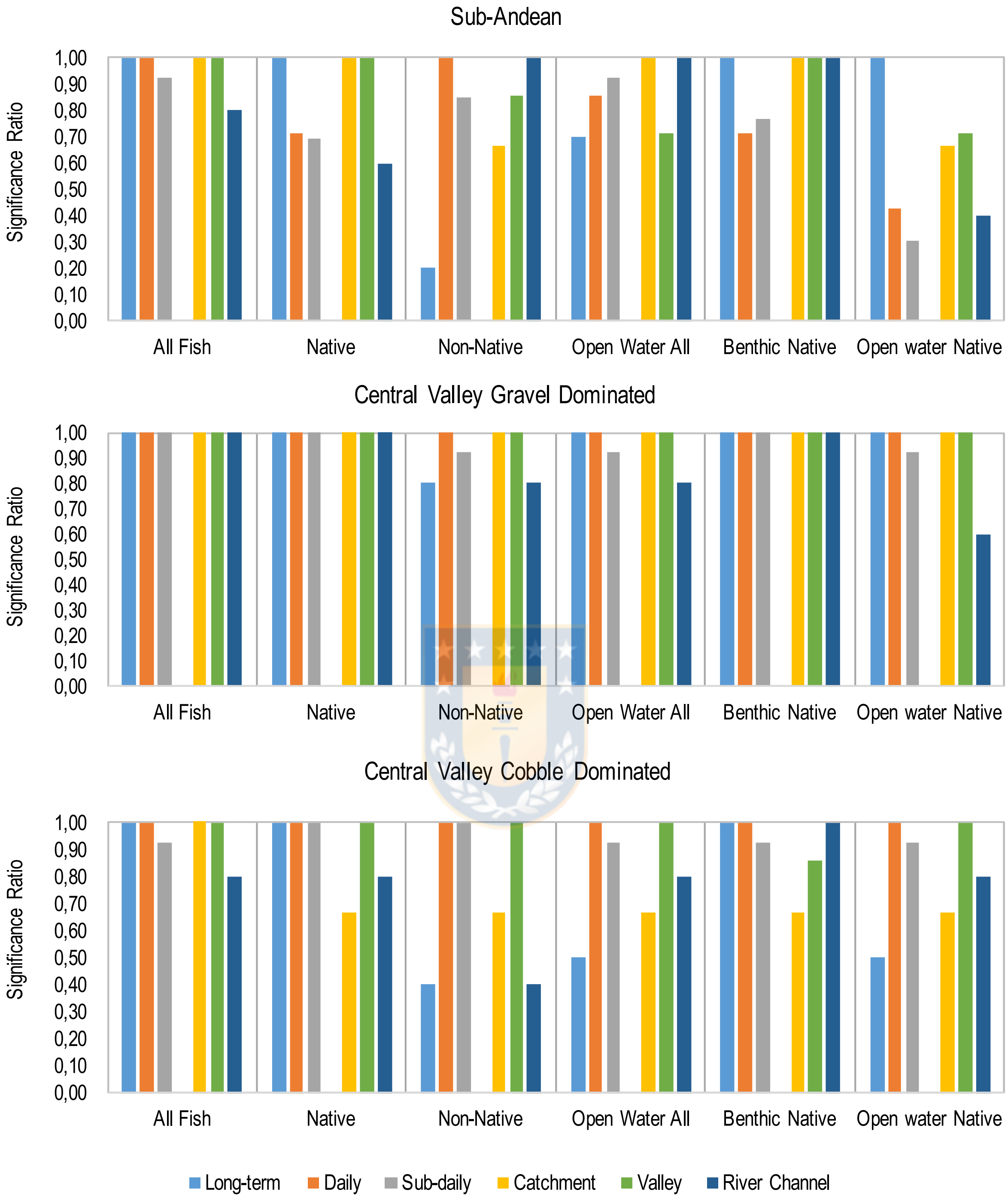

Figure 8.5. Hydrological and geomorphological drivers of fish assemblage structure at different ecological levels of organization in the Biobío and Imperial river. The significance ratio is the number of significant variables to the total number of variables used.

8.4 Discussion

Ecological responses are complex, and fish responses to flow management in the Biobío River resulted highly complex. To understand them, here we analyzed what changed, where and when, as well as how the changes occured. We found that fish are responding in a three-dimensional space, depending on the geomorphological, hydrological, and ecological level of organisation. First, fish response to flow regulation depends on the position within the river network or "where" the fish assemblage is. This position is spatial scale dependent; at the larger scale of the river network, the response is primarily mediated by FPZs. Then, within each FPZ, the fish assemblage response depends on the habitat type. Second, fish response is dependent on what ecological organization level is responding: all fish, native - no native, or benthic - open water species ("what"). Third, fish assemblage response is also timescale dependent, mediated by the age of the dams and the timescale of the hydrological variation. Notably, sub-daily hydrological variations resulted significant in explaining part of the fish response. Lastly, fish response was evidenced primary by abundances changes resulting in an increasing multivariate dispersion from natural flow regime to flow regulation. However, all assemblages subjected to the strongest flow regulation (hydropeaking) showed the same response, resulting in a homogenization at the river network scale. Therefore, the range of variability reduces at the ecosystem level, suggesting a potential loss of resilience at the network scale. Following, these results are discussed.

There were differences in fish assemblages across the six hydrogeomorphic zones located in high energy Andean river systems. The principal differences were observed through fish abundance at distinct ecological organisation levels that respond to main geomorphological and hydrological drivers at different hierarchical levels. The effect of flow regulation on fish abundance strongly depended on the position of the fish assemblage within the river network (FPZs or physical characteristics of the reach inhabited by fish), corroborating the strong influence of the geomorphic processes in shaping fish assemblages (Thoms et al., 2017). Therefore, the fish assemblage response not only depends on the adaptive character and species resilience to withstand the direct flow disturbances but primary, they are subordinate to the physical characteristics (geomorphology) and resilience to maintain their structure despite anthropogenic alterations.

Our results showed a hierarchical and complex fish response to flow regulation, in terms of what ecological organization level is responding and where in the river network. The responses of the highest ecological level that considers “all fish” occured at the river network scale at which large scale geomorphic variables together with the species intrinsic characteristics determined the responses of the fish assemblage (Thorp et al., 2008, 2006). When descending in ecological level, native and no native fish responses were observed at the scale of FPZs. No-native open water species (salmonids) were the most affected by hydropeaking in Sub-Andean FPZ, a highly energetic zone of the river, where native species are rare (Habit et al. 2006). On the other hand, native benthic species were the most affected fish group in Central Valley Gravel Dominated FPZ, where the river channel is wider, and differences in habitat availability favours the development of native fish groups, dominated by Siluriforms of the genera *Trichomycterus, Diplomystes* and *Bullockia* (Arratia, 1983; Habit et al., 2006; García et al., 2012). Furthermore, native open water fish species inhabit mainly in wide and young floodplains that are characteristic of the Central Valley Gravel Dominated FPZ. These areas are suitable for native fish such as *B. microlepidotus, C. galusdae* and *G. maculatus* that use them as spawning and juvenile rearing habitats (Montoya et al., 2012; Górski et al., 2018). However, in the same FPZ, but with hydropeaking flow regulation, these native fish abundances decreased.

Interestingly, fish response to flow management was primarily driven by abundance changes (assemblage structure). Thus, species richness and diversity index were not useful in disentangling the effect of hydro-geomorphology on riverine fish. In particular, the effects of different flow management on fish diversity (Shannon index) in the Biobío River basin was not significant. This could be explained by the low fish richness of Chilean rivers, which contrasts with a relatively high abundance of individuals within each species, typical to small-bodied species (Habit et al., 2006;

Vila & Habit, 2015). This singularity is typical to Andean rivers in Chile, and it is evident in the Biobío River basin even it is the most species-rich basin in the country (a total of 18 species; Vila et al. 2006). The low richness of freshwater fish in Chile (46 in total) is the result of the geological history, geographical isolation, as well as the physical characteristics of the Andean rivers, typically short, with high slope, and high energy (Campos, 1985; Vila et al., 1999; Vera Escalona et al., 2018).

In addition to abundances and community structure changes, multivariate dispersion of the fish assemblages revealed changes in the range of variability. Assemblages inhabiting areas with natural flow regime showed the highest dispersion range, meanwhile, communities in ROR areas presented the lower range. Therefore, communities in ROR areas are showing a loss of variability, suggesting than ROR is causing a homogenization of their fish assemblages. In the Biobío River, ROR hydropower plants are older than dams with hydropeaking (Ver CAPITULO II). Therefore, ROR flow alteration has a longer history, which could explain the stronger reduction in the dispersion range than in areas with hydropeaking. However, dams in the Biobío were constructed relatively recently (<45 years ago), and therefore, the changes in fish assemblages are recent and occurred rapidly. Comparison of the range of variability within FPZs with flow alteration, reduction was higher in Central Valley Gravel Dominated FPZ and Central Valley Cobble Dominated FPZ than in Sub-Andean FPZ. This reveal a stronger effect on native species, which are the dominant species in these FPZs.

Several studies suggest that variability changes of an ecosystems foreshadow ecological regime shifts (Kleinen et al. 2003; Scheffer & Carpenter, 2003; van Nes & Scheffer 2003; Brock et al. 2006; Carpenter and Brock, 2006). Evidence of this is shown in the Biobío River, where the variability of fish communities increases at multiple ecological levels in the hydrogeomorphic zones altered by hydropower. Meanwhile at the network scale the variance analysis indicated homogenization or loss of variability range in fish community structure. This increase of variability at the local scale and homogenization at the network scale may suggest that the system approaches a tipping point (sensu Scheffer et al., 2012.). At this state, perturbation even at a small-scale, can propel changes of the entire system toward an alternative state or cause systemic transition through cascading domino effect (Scheffer et al., 2012). This transition, in turn, causes loss of resilience of the system and as a consequence, the ecological system is transformed into less productive or otherwise less desired state (Folke et al., 2004).

Assessment of the interplay of hydrology, geomorphology and ecology in Andean high energy rivers emphasizes the importance of the location within the river network for the development of fish assemblage structure. In particular, the highest ecological level formed by all fish respond to network level related to catchment and valley variables and the responses are linked to where they are located within the network. In the next lower ecological level, native and non-native fish, the response occur at the level of river reach and FPZ (mesoscale). Here the importance lies in the physical characteristics of the channel besides its location in the river network. Finally, in the lowest ecological level, fish grouped according to their habitat preferences, responded at the microscale and the most important driver of these responses is linked to how stable their habitat is. This habitat stability, in turn, is driven by sub-daily flow variability and the consequences it has for geomorphology and ecology.

Our results highlight the importance of sub-daily flow variations in explaining the drivers of the differences in fish assemblages among the hydrogeomorphic zones. The hydrological variables at short temporal scales (sub-daily) revealed more stable character of flow in hydrogeomorphic zones with natural regime and highly variable flow in hydrogeomorphic zones altered by hydropeaking. These sub-daily flow changes caused severe decrease in abundance of native and non-native fish that inhabit open water in hydrogeomorphic zones with altered flow. This decline is probably caused by the influence of the sub-daily flow variations on key physical variables such as water depths and velocities as well as wetted area reductions that will impact the availability, stability and quality of open water fish habitat (Cushman, 1985; Blinn et al., 1995; Freeman et al., 2001; Shen & Diplas, 2010; Hauer et al., 2012). These variables have rapid changes causing habitat diversity reductions and changes in the stable aquatic and riparian habitat with ecological consequences as for fish assemblages as migration (Carmichael et al., 1998), feeding ability (Barwick and Hudson, 1985), and spawning success (Grabowsky and Isely, 2007), growth (Peterson and Jennings, 2007), recruitment (Rulifson and Manooch, 1990), fish mortality (Scruton et al., 2003), decreased abundance of young-of-year fishes and altering community composition (Freeman et al., 2001). This implies that establishing connections between high temporal resolution of flow metrics and sub-daily recording with geomorphic and ecological process is a crucial step and is urgent in order to manage or restore (semi-) natural flow regimes (Meile et al., 2011).

The present study advances our understanding of river networks by disentangling the effects of interplay of geomorphology and hydrology on fish assemblage structure. As such it also reinforces the necessity of an interdisciplinary research needed to advance understanding of rivers as ecosystems (Thoms et al., 2007). A focus on interaction of geomorphic, hydrological and ecological processes, and consideration of their hierarchical nature is essential (Dollar et al., 2008) and will allow to understand and model their responses to perturbations both natural and human induced. This understanding is instrumental for effective management of river systems in order to preserve their ecosystem services.

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9 DISCUSION

9.1 Zonas de procesos funcionales en los ríos Biobío e Imperial, perspectiva eco-geomorfológica en el modelo de estudio.

Los modelos conceptuales tienen como finalidad proporcionar un marco para comprender las funciones y procesos que ocurren en los ecosistemas (Allen & Starr, 1982; Allen et al., 1990; Thorp et al., 2008; Collins et al., 2014). Variados modelos conceptuales han intentado explicar de manera sencilla el comportamiento de los sistemas fluviales, con el fin de comprender los procesos y patrones que ocurren en estos ecosistemas (Vannotte et al., 1980, Montgomery, 1999; Thorp et al., 2008). En esta investigación, el marco conceptual Riverine Ecosystem Sinthesis (RES; Thorp et al., 2006, 2008) fue utilizado como un marco de referencia para comprender los patrones geomorfológicos longitudinales y laterales de las cuencas de los ríos Biobío e Imperial, siguiendo un análisis cuantitativo top-down para evaluar el carácter geomorfológico de dos ecosistemas fluviales andinos. Como resultado, las cuencas de estudio – Biobío e Imperial – presentaron en total siete zonas de procesos funcionales (FPZs) y, tal como lo predice la hipótesis RES, las FPZs en los ríos andinos estudiados, aparecen repetidamente en las cuencas y no muestran una distribución en un perfecto continuo longitudinal, según lo que predice el marco conceptual del río continuo (Vanotte et al., 1980), sino que su distribución se configura como una serie de parches a gran escala, sin una progresión ordenada aguas abajo de la cuenca.

Las zonas de procesos funcionales (FPZ) demostraron ser una fuerza principal en la estructuración de las comunidades de macroinvertebrados y peces. En cada una de las FPZs estudiadas, se observaron comunidades de macroinvertebrados y peces únicas. Así, por ejemplo, la FPZ Sub-Andean está compuesta principalmente por macroinvertebrados trituradores de materia orgánica y peces de origen no nativos que habitan la columna de agua. Mientras que, la FPZ denominada Central Valley Cobble Dominated se asocia con una alta riqueza de peces, donde la especie no nativa *Gambusia holbrooki* presenta una alta abundancia. La FPZ Central Valley Gravel Dominated se asocia con macroinvertebrados filtradores y ramoneadores y ensamble de peces principalmente de origen nativo con preferencias de hábitat tanto de columna de agua como bentónicos. Por último, FPZ Lowland se asocia con especies de peces nativas tales como, *B. microlepidotus, Percilia irwini y Galaxias maculatus*. Estos resultados demuestran la fuerte influencia de los procesos geomorfológicos en acomodar diferentes comunidades (Thoms et al., 2017) y concuerdan con otros autores que han demostrado que determinadas comunidades de macroinvertebrados y tramas tróficas se asocian al carácter espeífico de las FPZs (Maasri et al., 2019; Thoms et al., 2017; Boys & Thoms, 2006; Delong, Thoms y Sorenson, 2019). Todo ello coincide con lo postulado por la hipótesis de Riverine Ecosystem Synthesis, la que plantea que "la distribución de especies y la diversidad a nivel de comunidad, desde la cabecera hasta la desembocadura de un río reflejan la naturaleza de las FPZs" (Thorp et al., 2006).

Por último, una de las ventajas de incluir la perspectiva geomorfológica (FPZs) dentro del diseño de estudio fue la eliminación del sesgo existente en comparaciones equívocas de segmentos de río con distintas características físicas, historia hidrológica e historia sedimentaria y con ello se logró capturar y explicar la mayor variabilidad natural del sistema fluvial (McCluney et al., 2014).

9.2 Alteración de caudal en la cuenca del río Biobío y sus efectos en la biota acuática

La cuenca del río Biobío es una de las cuencas más extensas del país con 24.029 Km^2. Hoy en día, esta cuenca alberga 11 centrales hidroeléctricas dentro de su red hidrográfica, distribuida en los ríos Biobío, Duqueco, Rucúe y Laja. Una de las principales alteraciones que estas centrales hidroeléctricas provocan en la cuenca del río Biobío, es la alteración hidrológica, relacionada directamente con el tipo de operación predominante en cada una de ellas. Los tipos de operación utilizada por estas centrales hidroeléctricas son hydropeaking o tradicionalmente llamada de "punta" y run-of-river denominada como de "pasada o flujo base".

En esta investigación se caracterizaron 800 Km de red hídrica de la cuenca del río Biobío, tanto en términos geomorfológicos como hidrológicos. Del total de kilómetros estudiados, 230 Km (aproximadamente solo un tercio de la red hídrica) mantienen un régimen de caudal natural caracterizado por baja variabilidad de caudal diario y con cambios en la magnitud en su caudal diario que no superan los 11 m^3/s en 24 horas. Mientras que, 300 Km de los 800 Km estudiandos, mantienen un flujo alterado por la operación hydropeaking y 220 km por operación del tipo run-of-river. Las alteraciones en el caudal ocasionadas por las operaciones hydropeaking y run-of-river coinciden con las descritas por otros autores en distintos ríos del mundo (Almodüvar & Nicola, 1999; Bruno et al., 2013; Bejarano et al., 2017; Ashraf et al., 2018; Hecht et al., 2019; Giulivo et al., 2019). El hydropeaking, produce alta variabilidad de caudales de manera sub-diaria y fuertes cambios en la magnitud, frecuencia y tasa de cambio de los caudales sub-diarios y diarios. En 24 horas, este tipo de operación puede producir cambios de caudal promedio de 156 m^3/s. En tanto, la operación de tipo run-of-river incrementa la magnitud y frecuencia de caudal diario y sub-diario, con un cambio promedio de 26 m^3/s en 24 horas. Si bien este tipo de operación también genera un aumento de la variabilidad en los caudales sub-diarios, esta es menor a la generada por la operación de tipo hydropeaking. En cuanto a la estacionalidad anual de los caudales, y contrario a hallazgos de otros autores a lo largo del mundo (Chen et al., 2015; Loures & Pompeu, 2015; Mihalicz et al., 2019), en la cuenca del río Biobío, no se observan cambios a esta escala, sino que el hidrograma anual muestra la mantención de los patrones estacionales de caudal. Esto es el resultado de la baja capacidad de almacenamiento de los embalses instalados en la cuenca del río Biobío, menor a los caudales que ocurren en la temporada de invierno, por lo que no logran almacenar esta cantidad de agua para su liberación en verano. En cuanto a la distribución espacial de las centrales hidroeléctricas, se registró que la operación de tipo hydropeaking, se encuentra principalmente distribuida en las FPZs Sub-Andean y Central Valley Gravel Dominated, mientras que la operación de tipo run-of-river afecta la FPZ Central Valley Cobble Dominated en su totalidad.

Tal y como ha sido expresado por varios autores (Petts, 1980; Poff et al., 1995; Bruno et al., 2013), la alteración hidrológica generada por las centrales hidroeléctricas desencadena importantes impactos negativos tanto en las comunidades de macroinvertebrados como de peces. En conformidad a ello, la cuenca del río Biobío exhibe una disminución significativa de la abundancia de macroinvertebrados y peces en las secciones del río sometidas a regulaciones del caudal del tipo hydropeaking, como también una reducción de la riqueza de especies en el caso de macroinvertebrados. Para ambos grupos biológicos, se detectaron rasgos funcionales menos tolerantes a la alteración de caudales, los que responden de forma pronunciada a los efectos de la regulación de caudal. Entre ellos se encuentran, trituradores y filtradores en macroinvertebrados, como también aquellos peces que habitan la columna de agua (*B. microlepidotus, C. galusdae y G. maculatus*) y de hábitat bentónicos (*D. nahuelbutaensis y G. australis*). Los mecanismos impulsados por la regulación de caudal que parece explicar mejor la disminución en la abundancia de los grupos con estos rasgos funcionales son la deriva catastrófica, los cambios en la disponibilidad y calidad del hábitat, las alteraciones en la calidad de agua y los cambios en la disponibilidad de alimento (Bunn & Arthington, 2002). En el caso específico de *G. australis*, el efecto de la fragmentación puede ser también un forzante mayor, dado su ciclo de vida anádromo (Díaz et al. 2019). El hydropeaking produce el desplazamiento forzoso de organismos hacia aguas abajo (deriva catastrófica), mediante el aumento de la velocidad de corriente (García et al., 2011; Herland, 2012), cambios de temperatura (Carolli et al., 2012) y aumento en el transporte de sedimentos del lecho del río (Gibbins et al 2007; Schülting et al 2016, 2018; Vericat et al., 2020). La deriva catastrófica por lo general es documentada para invertebrados (Bruno et al., 2012; Herland, 2012; Schülting et al., 2016; Schülting et al., 2018; Céréghino & Lavandier, 1998; Céréghino et al., 2002; Moog, 1993), no obstante, también es posible su ocurrencia en peces pequeños o larvas de peces (Zitek et al., 2004; Schmutz et al., 2015).

La disponibilidad y la calidad del hábitat físico es una variable determinante para el desarrollo de la historia de vida de las especies (Maddock, 1999). Por ello, los cambios bruscos y persistentes en las condiciones hidráulicas del hábitat (velocidad, profundidad, constricción hábitat), generan efectos directos sobre la biota acuática (Bunn & Arthington, 2002). Sobre esto se ha descrito que, los cambios repentinos en la velocidad de corriente generados por la operación hydropeaking, puede producir el varamiento de macroinvertebrados y peces (Cabaltica et al., 2013; Halleraker et al., 2003). Además, la disminución de la profundidad del agua, y constricción del hábitat, descrito en aquellos periodos de baja demanda energética y por consiguiente bajos caudales en los ríos, ocasionan una continua desecación de las orillas de los ríos. Todas estas condiciones exponen a macroinvertebrados y peces a desecación y asfixia, reducción en la cantidad de hábitat de desove disponible y somete los huevos a la desecación y al daño debido a la radiación solar directa (Moog et al., 1993; Valentin et al., 1995; Kennedy et al., 2006; Grabowski e Isely 2007; Theodoropoulos et al., 2015; Poff y Schmidt 2016; Melcher et al 2017). Esto último es especialmente importante para peces nativos de las cuencas andinas, dado que la oviposición de huevos de varias especies ocurre en pozas someras de las planicies de inundación de los ríos (Montoya et al., 2012).

Las fluctuaciones diarias del nivel del agua pueden inducir fuertes cambios en la calidad del agua en las secciones reguladas, con variaciones bruscas en la temperatura, oxígeno y en las concentraciones de sólidos suspendidos en el agua. Estas variaciones en los parámetros fisicoquímicos son trascendentales para la supervivencia de especies vulnerables a los cambios en la calidad de agua, tales como trituradores y EPT, grupos sensibles a la disminución del oxígeno y aumentos de la temperatura o bien filtradores expuestos a daños en sus dispositivos de alimentación por el aumento de sedimentos suspendidos en el agua (Moog et al 1993; Englund & Malmqvist, 1996; Calapez et al 2018).

Por último, se espera que la menor disponibilidad de alimento sea una variable importante que determine las abundancias de especies en las redes fluviales. En este sentido, se ha descrito la reducción de la abundancia de macroinvertebrados trituradores en ríos, debido a la inestabilidad de la hojarasca producida por las variaciones de caudal y aumento de la velocidad del agua producen, (Schade &

Fisher, 1997, Casas et al., 2014). Como consecuencia, se espera que, aquellas especies que basan su dieta en macroinvertebrados bentónicos, se vean fuertemente reducidos en sus abundancias en tramos con hydropeaking (Englund & Malmqvist, 1996).

9.3 Implicancias ecológicas a nivel de cuenca de la alteración hidrológica.

Tres principales resultados obtenidos en este estudio tienen implicancias a nivel de cuenca hidrográfica, en la cuenca del río Biobío: 1) Extensión espacial de las alteraciones hidrológicas, 2) cambios en la estructura comunitaria de peces y macroinvertebrados y 3) aumento de la variabilidad en los niveles ecológicos evaluados, tanto de macroinvertebrados y peces, a escala de zonas hidrogeomorficas. Además, homogenización o pérdida del rango de variabilidad en la estructura de la comunidad peces a escala de cuenca.

Gran parte de la extensión longitudinal estudiada, correspondiente a los principales ríos de la cuenca del río Biobío (río Biobío, Duqueco, Huequecura, Laja y Rucúe), se encuentran actualmente con alteraciones hidrológicas (495 Km). Las alteraciones de caudal, primordialmente aquellas producidas por la operación de tipo hydropeaking son observables fuera de los límites reconocidos en sus evaluaciones ambientales como su área de influencia. Por lo que es claro que los impactos que este tipo de operación tiene sobre los caudales del río, hábitats y biota acuática se han subestimado en todas las evaluaciones de impacto ambiental. A nivel de FPZs, se observa que las zonas ubicadas en el valle se encuentran alteradas en su caudal en gran parte o totalidad de su extensión (Central Valley Cobble and Gravel Dominated). Ello que implica que estas zonas poseen un funcionamiento no natural, con procesos físicos tales como, régimen de caudal y transporte de sedimentos, totalmente modificados. Esta modificación, tiene consecuencias directas en el número, distribución, diversidad y conectividad de los parches hidrogeomórficos que componen cada FPZ. A su vez, la pérdida de parches y la conectividad entre ellos dentro de cada FPZ resulta en alteraciones de los procesos ecológicos que ocurren en cada FPZ, tales como, la alteración de los ciclos de vida de las especies, especialmente los peces, dado que muchos organismos dependen de la existencia de múltiples parches para el desarrollo de sus ciclos, entre ellos es posible mencionar la alimentación, reproducción y anidamiento (Montoya, et al., Melcher et al., 2016; Bejarano et al., 2014; Vivancos et al., 2020). Esta información es de toda importancia en términos de manejo de la cuenca del río Biobío, dado que nuestros resultados revelan que aquellas FPZs ubicadas en el valle - en estado natural - poseen la mayor riqueza y abundancia de especies de peces nativos, no obstante, hoy en día sus ensambles se encuentran en riesgo producto de las alteraciones de caudal.

En relación con los ensambles de macroinvertebrados y peces, esta investigación demostró una clara tendencia general a la disminución de las abundancias en ambos ensambles en las secciones del río con alteración hidrológica, independiente de la FPZ. Solo en casos excepcionales, como el del ensamble de macroinvertebrados ramoneadores (scrapers) se observó el aumento de sus abundancias en zonas con alteración. En concreto, el ensamble trófico de trituradores y filtradores para macroinvertebrados y los peces que habitan la columna de agua (*B. microlepidotus, C. galusdae y G. maculatus*) y de hábitat bentónicos (*D. nahuelbutaensis y G. australis*) ven drásticamente disminuidas sus abundancias en las secciones del río con alteración hidrológica. Ahora bien, es interesante señalar que las reducciones más pronunciadas de abundancia se reflejan en aquellas FPZs donde naturalmente son más abundantes (ej. trituradores y salmónidos en Sub-Andean FPZ y filtradores y peces nativos en Central Valley Gravel Dominated FPZ). Por lo que, el efecto de la regulación del caudal sobre la abundancia de los ensambles de macroinvertebrados y peces dependen en gran medida de la posición de los ensambles en la red fluvial (zonas de procesos funcionales o características físicas del tramo habitado), lo que corrobora la fuerte influencia de los procesos geomorfológicos en la conformación de las comunidades (Thoms et al., 2017).

Por otro lado, esta investigación enfatiza la interacción de las variables hidrológicas y geomorfológicas en la estructuración de los ensambles de macroinvertebrados y peces. Además, los resultados evidencian la importancia de la escala temporal de las variables hidrológicas y de la escala espacial de las variables geomorfológicas. En específico, las variables de caudal a escala temporal corta (sub-diario) estructuraron los ensambles de macroinvertebrados y peces, en todos los niveles ecológicos de organización. En cuanto a la geomorfología, y opuesto a lo que se esperaba, las variables de escala del canal del río no fueron significativas como impulsoras de la estructura del ensamble de macroinvertebrados en las dos zonas de procesos funcionales estudiadas en ese caso, pero si lo fueron para peces con preferencias de hábitat asociadas a la columna de agua.

Los cambios en la estructura ecológica del río Biobío, puede tener altos costos para el sistema fluvial, tales como, pérdidas de biodiversidad y desequilibrios en los ciclos biogeoquímicos de la cuenca, los cuales podrían afectar negativamente las propiedades y servicios del ecosistema (Dugan et al., 2010; Auerbach et al., 2014). En específico, la disminución de la abundancia y en algunos casos la extirpación, de macroinvertebrados pueden tener una influencia importante en los ciclos de nutrientes, la productividad primaria, la descomposición y la translocación de materia orgánica (Palmer & Ruhi, 2019). La disminución de trituradores en la sección más alta de la cuenca se relaciona con la disminución longitudinal de la biomasa detrítica, que sustenta a macroinvertebrados colectores y filtradores (Heard & Richardson, 1996). Además, la pérdida de filtradores significa la pérdida de las dos funciones primordiales de este grupo trófico que son la reducción de la materia orgánica fina en suspensión y el suministro de partículas más grandes a través de sus heces a un amplio espectro de detritívoros que se alimentan de sus depósitos (Wallace, 1996). Sumado a ello, la pérdida de depredares tope, tales como peces, influirá en el control top-down en las cadenas tróficas de los ríos, facilitando la permanencia de ciertas especies sobre otras (Ruetz et al., 2002; Winemiller et al., 2014).

Estos resultados sugieren que la alteración de caudales ha producido, a escalas de FPZs, aumento en la variabilidad de las comunidades de peces y macroinvertebrados a múltiples niveles ecológicos. Estos resultados, han sido descritos por varios autores como un indicio de cambios en el régimen ecológico para sistemas acuáticos y terrestres (Schlesinger et al. 1996; van Nes & Scheffer 2003; Oborny et al. 2005; Brock & Carpenter, 2006; Scheffer et al., 2012). En este estado, una perturbación, incluso a pequeña escala, puede impulsar el cambio de todo el sistema hacia un estado alternativo a través de un efecto dominó en cascada (Scheffer et al., 2012). Todo esto, implicaría que el sistema fluvial sea más vulnerable a cambios ambientales, disminución de la resistencia y/o resiliencia a las perturbaciones y que ocurran pérdidas de servicios ecosistémicas (ciclos de nutrientes y producción de peces, respectivamente (Folke et al., 2004).

En base a los resultados obtenidos de esta investigación, se aceptan los siguientes enunciados de la hipótesis: Se confirma que las zonas de procesos funcionales acomodan ensambles de macroinvertebrados y peces únicas. Se constata que las centrales hidroeléctricas instaladas en la cuenca del río Biobío alteran los caudales naturales de los ríos donde se ubican, con efectos negativos sobre las comunidades de macroinvertebrados y peces, tales como, reducción de las abundancias de macroinvertebrados y peces en aquellas secciones de río con alteración hidrológica. Se determina que, los macroinvertebrados triturados y filtradores como los peces de hábitat de columna de agua son los grupos que muestran las mayores reducciones en sus abundancias. Por último, las variables hidrológicas a escala temporal corta (sub-diaria) explican la configuración y respuestas de la estructura de ensambles de macroinvertebrados y peces. No obstante, y contrario a lo descrito en la hipótesis, las variables geomorfológicas a escala espacial pequeña (canal) solo presentaron un rol relevante para los ensambles de peces y no para macroinvertebrados. Para estos últimos se observó que las variables geomorfológicas a meso-escala influyen en las respuestas de estos ensambles a la alteración de caudal.

Por último y a la luz de los resultados presentados sugerimos cuatro aspectos importantes a considerar para la gestión de la instalación y operación de centrales hidroeléctricas:

a) Las condiciones hidrogeomorfológicas de la cuenca.

El impacto del hydropeaking depende en gran medida de la hidrogeomorfología de las secciones del río afectadas por la regulación del caudal (Parasiewicz et al., 1998; Vanzo et al., 2016). En este sentido, nuestros resultados respaldan que los ensambles de macroinvertebrados y peces se ven mayormente afectados por el hydropeaking en zonas ubicadas en el valle de los ríos, por lo que, la instalación de centrales hidroeléctricas no es del todo recomendable en estas zonas de procesos funcionales. Por otro lado, y en consistencia a lo descrito por Laborde et al., 2020, en las zonas altas de las cuencas, donde en particular se ubica la zona de proceso funcional Andean y Sub-Andean, se observa que los ensambles de peces y macroinvertebrados serían más resilientes a las alteraciones del caudal provocadas por el hydropeaking.

b) Considerar las especies y sus rasgos funcionales.

Nuestros resultados y la literatura indica que algunas especies son más vulnerables que otras a las alteraciones del caudal provocadas por el hydropeaking. Por lo tanto, es del todo necesario que los diseños de mitigación seleccionen las especies con mayor sensibilidad a las fluctuaciones artificiales del caudal, asumiendo que todas las demás especies estarán indirectamente protegidas. Esta selección realizada en base a sus rasgos funcionales, patrones de historia de vida y estado de conservación.

c) Umbrales de hydropeaking

Las medidas de mitigación de tipo operativas que implican la manipulación de los caudales artificiales se convierten en un imperativo. En detalle, los atributos del régimen de caudal - magnitud, la duración, la frecuencia, la relación de flujo y la tasa de cambio de flujo - están relacionados con distintas respuestas ecológicas que pueden utilizarse para definir umbrales de mitigación, cuyo diseño debe tener en cuenta las especies clave y sus requisitos ecológicos. Por lo que, se sugiere una mesa de trabajo en conjunto con limnólogos, geomorfólogos e hidrólogos para ver las factibilidades de reducir fluctuaciones de caudal, abarcando aquellos parámetros o atributos hidrológicos de mayor relevancia para las especies. Por ejemplo, las reducciones de caudal máximo, combinadas con liberaciones de un caudal mínimo óptimo son una recomendación común de mitigación para reducir la mortalidad en los primeros estadios de vida de macroinvertebrados y peces como también la desecación de los individuos en la orilla de los ríos.

d) Crear y ejecutar protocolos de monitoreo de biodiversidad:

Efectos negativos a distintas escalas ecológicas, fueron observados sobre el ensamble de macroinvertebrados y peces a causa de la alteración de caudales. No obstante, se necesitan protocolos de monitoreo de biodiversidad a largo plazo para comprender la dinámica temporal de las especies biológicas como también monitoreos e investigaciones que aborden los patrones de historia de vida de las especies con el fin de generar medidas de mitigación y conservación apropiadas.

10 CONCLUSIONES

El desarrollo de esta investigación generó información relevante sobre los efectos de la operación de las centrales hidroeléctricas sobre las comunidades de macroinvertebrados y peces. Estos efectos, están directamente relacionados con el tipo de operación ejecutada por las centrales hidroeléctricas y las zonas de procesos funcionales donde se modifica el caudal. A continuación, se describen las principales conclusiones para cada capítulo

Capitulo I.

- Sobre la base del análisis geomorfológico a escala de cuenca, valle y canal se documenta la existencia de zonas de procesos funcionales específicas dentro de las cuencas de los ríos Biobío e Imperial.
- Siete zonas de procesos funcionales emergen del análisis realizado, de las cuales, cuatro están presentes en las cuencas del río Biobío e Imperial (Sub-Andean, Central Valley Cobble Dominated, Central Valley Gravel Dominated, Lowland)
- Tres zonas de procesos funcionales se localizan exclusivamente en una de las cuencas de estudio, en específico dos zonas se localizan en la cuenca del río Biobío (Andean y Reservoir) y una exclusivamente en la cuenca del río Imperial (Tortuous Alluvial)
- Las zonas de procesos funcionales en la cuenca del río Biobío, presentan comunidad de peces particulares y únicas.

Capitulo II.

- El 34 % de la red hídrica estudiada en la cuenca del río Biobío presenta un régimen de caudal no natural regulado por centrales hidroeléctricas.
- En la red hídrica de la cuenca del río Biobío se encuentran tres categorías de régimen de caudal, denominadas caudal natural, run-of-river y hydropeaking.

- El hydropeaking produce fuertes alteraciones a escala temporal sub-diaria y diaria, sin embargo, no interviene en los patrones anuales del caudal.
- La operación de tipo run-of river, produce un aumento en la variabilidad de los caudales diarios y sub-diarios en los tramos analizados, pero en una magnitud menor a las registradas por operación de tipo hydropeaking.
- En la cuenca del río Biobío, las zonas de procesos funcionales Sub-Andean y Central Valley Gravel Dominated presentan mayoritariamente alteración de tipo hydropeaking. Mientras que la zona de proceso funcional Central Valley Cobble Dominated presenta alteración de tipo run-of-river.

Capitulo III.

- La alteración hidrológica ocasionada por el hydropeaking genera efectos negativos significativos sobre la estructura de los ensambles de macroinvertebrados.
- La abundancia de macroinvertebrados disminuye significativamente en sitios con hydropeaking en las dos zonas de procesos funcionales estudiadas.
- La disminución de abundancia ocurre para todos los niveles de organización ecológica estudiados, excepto para el grupo funcional de ramoneadores, los cuales aumentan su abundancia en las zonas sometidas a hydropeaking.
- Macroinvertebrados de rasgo funcional, tales como, triturados se ven mas afectados en su abundancia en la zona de proceso funcional Sub-Andean y filtradores en Central Valley Gravel Dominated.
- La varianza de la abundancia de macroinvertebrados fue significativamente mayor en los sitios de hydropeaking en ambas zonas de procesos funcionales.
- Las variables hidrológicas de escala temporal corta (sub-diaria) son forzantes primarios para el ensamble de macroinvertebrados en sistemas fluviales afectados por hydropeaking.
- Entre las variables geomorfológicas, las variables a escala de valle parecieron determinar la estructura del ensamble de macroinvertebrados, en ambas zonas de procesos funcionales

Capitulo IV.

- Las comunidades de peces presentan una compleja respuesta a la regulación de caudal, la cual está modulada primariamente por la posición de la comunidad dentro la red hídrica.
- Nuestros resultados mostraron que los ensambles de peces tienen una respuesta jerárquica y compleja a la regulación del caudal, en términos de que nivel de organización ecológica respondió a la alteracion del caudal y en qué lugar de la red fluvial ocurrió esa respuesta. En este sentido, especies nativas que habitan en la columna de agua y de hábitat bentónicos fueron más afectadas por el hydropeaking en FPZs ubicadas en la zona del valle, mientras que especies no nativas en FPZs de geomorfología confinada.
- Los principales forzantes de los complejos cambios de las comunidades de peces son variables hidrológicas de escala sub-diaria.

Conclusión global

- Las respuestas ecológicas a las alteraciones de caudal son complejas y son el resultado de la interacción de cambios en variables geomorfológicas e hidrológicas a distintas escalas espacio-temporales, las cuales a su vez afectan de manera distinta a las diferentes especies y grupos funcionales.
- Las centrales hidroeléctricas instaladas en la cuenca del río Biobío generan efectos adversos sobre las comunidades de macroinvertebrados y peces, los que dependen del tipo y magnitud de la alteración del régimen de caudal. Los grupos funcionales de macroinvertebrados más afectados corresponde a trituradores en Sub-Andean y filtradores en Central Valley Gravel Dominated FPZ y de peces corresponden a no nativos en Sub-Andean FPZ y nativos de columna de agua y bentónicos en Central Valley Gravel Dominated FPZ.
- La regulación de caudales en la cuenca del río Biobío ha implicado la total alteración de la zona de proceso funcional Central Valley Cobble Dominated,

ubicada en el río Laja, donde sus comunidades de peces han tendido a homogenizarse y por ende a perder resiliencia.

- Los complejos efectos ecológicos descritos en esta tesis sobre distintas especies y grupos funcionales no son considerados en los estudios de impacto ambiental de centrales hidroeléctricas, lo cual demuestra que los impactos predichos han sido, y siguen siendo, completamente subestimados.

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GLOSARIO.

Concepto	Definición
Caudal	Volumen de agua que pasa por una determinada sección transversal en la unidad de tiempo, generalmente se expresan en m^3/s.
Velocidad	Relación entre el espacio que recorre un cuerpo y el tiempo que tarda en recorrerlo. Si la distancia se expresa en metros y el tiempo se mide en segundos, entonces la velocidad queda indicada en m/s (cantidad de metros recorridos en un segundo). La proporción existente entre el caudal pasante y el area transversal al flujo.
Volumen	Unidad de medida de un cuerpo. Cantidad de agua en m^3 que ocupa el agua en el cauce.
Zonas de Procesos Funcionales	Unidad geomórfica fluvial entre valle y tramo
Composición comunitaria	Caracterización biológica de una localidad. Especies presentes en un sitio o localidad en un determinado momento.
Historia de vida	Secuencia de eventos relacionados con el crecimiento, sobrevivencia y reproducción de los individuos de una especie y que ocurren desde su nacimiento y muerte.
Homogenización	Incremento en la similitud de cualquier de tipo de medida de biodiversidad. Puede ocurrir en múltiples niveles de organización ecológica.